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Interactions between two invasive crab predators, Carcinus maenas and Hemigrapsus sanguineus, and consequences for the native community

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INTERACTIONS BETWEEN TWO INVASIVE CRAB PREDATORS, *Carcinus maenas* AND *Hemigrapsus sanguineus*, AND CONSEQUENCES FOR THE NATIVE COMMUNITY

BY

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ABSTRACT

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Carcinus maenas AND *Hemigrapsus sanguineus*,

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by

Blaine David Griffen

University of New Hampshire, May, 2007

With continued globalization, species are being transported and introduced into novel habitats at an accelerating rate. As invasive species become more common, interactions between invasive species will also increase and may alter the way that these species impact invaded communities. The European green crab *Carcinus maenas* is an aggressive predator that was introduced to the east coast of North America in the mid 1800s and often has detrimental impacts on prey communities. A newer invasive predator, the Asian shore crab *Hemigrapsus sanguineus*, was first discovered on the Atlantic coast in the 1980s, and now inhabits many of the same regions as *C. maenas* within the Gulf of Maine. It too can have significant negative impacts on prey communities. Interactions between these species are often aggressive and may alter their influences on native prey.

I used field and laboratory experiments together with spatial patterns in the field to investigate the impacts of these species and examine how interactions between them alter these impacts. My study focused on three interrelated areas of community ecology: multiple predator effects, prey dependent vs. ratio dependent foraging, and species

redundancy. I demonstrate that aggressive interactions between and within these species strongly influence their impacts on native communities. The result is that when both species are present, their combined impacts are less than the sum of their individual impacts. However, the strength of interference varied with habitat type, prey density, predator density, and size of predators that interacted.

Interference also affected predation by the two species differently, resulting in very different community impacts in areas where *C. maenas* dominates (northern Gulf of Maine) and areas where *H. sanguineus* has replaced *C. maenas* as the dominant predatory crab (Long Island Sound and southern Gulf of Maine, but progressing northward). Both conspecific and heterospecific interference strongly affected *C. maenas*, likely limiting its population size and subsequent impacts. In contrast, interference had little influence on predation by *H. sanguineus*. The lack of interference effects likely have allowed *H. sanguineus* to achieve very high densities observed in many areas, resulting in large population impacts on the native community.

INTRODUCTION

Invasion of marine habitats by nonindigenous species is of increasing global concern (Ruiz et al. 1997) with significant ecological and evolutionary implications for native populations (Grosholz et al. 2000, Cox 2004). Interactions between native and invasive species are common, and influence not only native communities, but also the success and impact of the invading species (e.g., Herbold and Moyle 1986, Robinson and Wellborn 1988, Baltz and Moyle 1993, Reusch 1998, Crawley et al. 1999, Byers 2002, deRivera et al. 2005). In addition to interactions with native species, interactions between invasive species may also alter their impacts on invaded systems (Simberloff and Von Holle 1999). Interactions between invasive species will likely become more frequent as the proportion of species that are invasive within communities increases. I have examined interactions between two species of invasive predatory crabs, the European green crab *Carcinus maenas* and the Asian shore crab *Hemigrapsus sanguineus*. Specifically, I have examined how interactions between these species alter their impacts on native prey, both at the level of the individual prey species and across several major components of the prey community. I have further examined the implications for the native prey of replacing *C. maenas* with *H. sanguineus* within invaded habitats, as has been observed in numerous locations (Lohrer and Whitlatch 2002a, Kraemer et al. In Press).

To examine these issues, I have framed my work in terms of two broad issues in ecology, multiple predator effects and species redundancy. Below I outline the invasion

history of *C. maenas* and *H. sanguineus*, highlighting previous work on impacts of and interactions between these species. I then briefly introduce the concepts behind multiple predator effects and redundancy in the impacts of different species.

Invasion Histories

Carcinus maenas

C. maenas has invaded multiple sites globally, including the east and west coasts of North America, South Africa, and Australia (Grosholz and Ruiz 1996). It was first noted on the Atlantic coast of North America in New York and New Jersey in 1817 (Say 1817). Since its invasion it has steadily spread northward, reaching the Gulf of Maine by the early 1900s (Rathburn 1905), then spreading up the coast of Maine and into Canada over the next half century (Scattergood 1952, Glude 1955). The current geographic range of *C. maenas* is from Nova Scotia to Maryland, and while *C. maenas* continues to expand the northern boundary of this range (Audet et al. 2003), its abundance in southern areas has been limited by predation from the larger native blue crab *Callinectes sapidus* (deRivera et al. 2005), and interactions with *H. sanguineus* (Lohrer and Whitlatch 2002a).

C. maenas is a voracious predator that can have broad predatory impacts on benthic communities in both soft sediment (Thrush 1986, Raffaelli et al. 1989, Fernandes et al. 1999, Whitlow 1999, Grosholz et al. 2000) and rocky intertidal sites (Tyrrell et al. 2006). While *C. maenas* will consume a wide variety of prey types (Ropes 1968, Elner 1981, Ropes 1989), it has a strong dietary preference for mollusks, and thus can have large impacts on bivalve prey (Glude 1955, Ebling et al. 1964, Richards et al. 1999,

Whitlow 1999). In addition to direct trophic impacts, *C. maenas* has indirectly influenced the invaded intertidal community by changing behavioral and morphological traits of native species (e.g., Appleton and Palmer 1988, Palmer 1990, Trussell et al. 2003).

Hemigrapsus sanguineus

Recently, *H. sanguineus*, has invaded much of the same region along the east coast of North America. First documented in New Jersey in 1988 (Williams and McDermott 1990), *H. sanguineus* rapidly spread its range from the Gulf of Maine to North Carolina in less than a decade (McDermott 1998a). Since its arrival to the Gulf of Maine in the late 1990s, *H. sanguineus* has continued to spread northward and to increase in density, though at a slower pace. The current northern limit of *H. sanguineus*' range is mid-coast Maine; however, the ultimate extent of its invasive range is uncertain. Native populations in the western Pacific span a range equivalent in latitude to a range on this coast from the Gulf of St. Lawrence to Cuba (McDermott 1998a and references therein). However, its eventual invaded range may be somewhat smaller due to limitations imposed by advective currents in the north (Byers and Pringle 2006) and a lack of preferred hard substrates in the south.

H. sanguineus has a broad diet that includes both plant and animal material (McDermott 1998b, Tyrrell and Harris 1999, Lohrer et al. 2000, Ledesma and O'Connor 2001). Laboratory food preference trials indicate that individual *H. sanguineus* have a strong preference for bivalve prey (Brousseau and Baglivo 2005 and Griffen, unpubl. data). However, gut contents of naturally foraging crabs indicate that plants and animals

contribute fairly evenly to *H. sanguineus*' diet (Lohrer et al. 2000). The broad nature of *H. sanguineus*' diet implies that its impacts on the invaded community may be correspondingly broad (Tyrrell and Harris 1999). Further, because *H. sanguineus* can achieve very high population densities (Brousseau et al. 2003), its impacts may even be stronger than those of *C. maenas* (Lohrer and Whitlatch 2002b). In contrast to *C. maenas*, indirect influences of *H. sanguineus* caused by changing traits of native species appear to be spatially variable, and may depend on the length of time that *H. sanguineus* has been present in a site (Freeman and Byers 2006).

Interactions Between *C. maenas* and *H. sanguineus*

C. maenas is generally found in a broader range of habitats (soft sediment, marsh, subtidal, etc.) than *H. sanguineus*. However, both species are abundant in rocky intertidal habitats. Early studies that documented the distribution of and resource use by *H. sanguineus* noted the extensive overlap between these species and suggested that competitive interactions may occur (McDermott 1998a). And indeed, competition with *H. sanguineus* reduces use of refuge habitat (rocks) by juvenile *C. maenas*, and also alters foraging success (Jensen et al. 2002).

On the regional scale, the densities and distributions of these two species have shifted dramatically over the last decade as the introduction of *H. sanguineus* appears to have decreased the numbers of *C. maenas* in rocky intertidal habitats where *C. maenas* was once abundant (Lohrer and Whitlatch 2002a, Kraemer et al. In Press). Several mechanisms may potentially explain this species replacement, including predation by *H. sanguineus* on settling *C. maenas* megalopae (Lohrer and Whitlatch 2002a), displacement

of juvenile *C. maenas* from refuge habitat (Jensen et al. 2002) and subsequent increased predation mortality, and/or food competition given similar diets (Ropes 1968, Elner 1981, McDermott 1998b, Tyrrell and Harris 1999, Lohrer et al. 2000). Whatever the mechanism(s), densities of *C. maenas* within the Gulf of Maine are declining as *H. sanguineus* densities increase (Griffen, pers. obs.), similar to what was observed in Long Island Sound (Lohrer and Whitlatch 2002a, Kraemer et al. In Press).

Displacement of *C. maenas* by the advancing *H. sanguineus* invasion has resulted in a region of overlap between the species that has steadily shifted northward. This region encompassed the New Hampshire coast throughout the duration of this study, and both species were found abundantly at Odiorne Point, the location of the majority of my field work. This is a relatively sheltered site on the outer coast of New Hampshire that is characterized by a series of coves, each separated by rock outcroppings. Flora and fauna at this site have a relatively low species diversity, typical of New England intertidal habitats (Menge 1976), that have been extensively documented by Tyrrell (2002). This low diversity provided an excellent opportunity both to isolate interactions between a limited number of focal species, and to examine effects of these invaders across the broader prey community.

The invasions by these species and subsequent interactions have provided an ideal opportunity to examine several important ecological questions. My investigations, while examining specific interactions between these two invasive crabs, have focused more broadly on three interrelated areas of community ecology: multiple predator effects, prey dependent vs. ratio dependent foraging, and the functional similarity or redundancy of species. Below I briefly discuss these three topical areas that my research addresses.

Areas of Investigation

Multiple Predator Effects

Predation is an important force in natural communities that can control the abundance of prey directly (Hairston et al. 1960, Sih et al. 1985) and can also influence the structure and dynamics of the broader community by altering other community-structuring forces such as competition (Paine 1966). Research over the last two decades has demonstrated the complexity of natural predator-prey systems, highlighting interactions between predator species that share the same prey resources (Sih et al. 1998). Predation rates of predators that share a common resource frequently do not combine additively. Rather, multiple predator species often combine to cause synergistic (risk enhancement) or compensatory (risk reduction) prey mortality. Both of these impacts are broadly termed emergent multiple predators effects (Sih et al. 1998).

Understanding factors that influence the direction (synergistic or compensatory) and magnitude of multiple predator effects is necessary for understanding the structure of natural communities and for managing the dynamics of exploited ecosystems. Work to date has demonstrated that risk enhancement may be expected in systems where prey responses to the first predator species increase the susceptibility to the second (Soluk 1993, Losey and Denno 1998, Swisher et al. 1998, Eklöv and VanKooten 2001, DeWitt and Langerhans 2003, Harvey et al. 2004), while risk reduction may be expected in systems where predator interference or intraguild predation (predation among predators that share the same prey) are common (Peckarsky 1991, Soluk 1993, Eklöv and Werner 2000, Finke and Denno 2002, Crumrine and Crowley 2003, Lang 2003, Warfe and Barmuta 2004). However, relatively few studies have attempted to detect either patterns

in the strength of risk reduction or risk enhancement or mechanisms that may alter their strengths (but see Soluk 1993, Losey and Denno 1998, Finke and Denno 2002, Warfe and Barmuta 2004, Vance-Chalcraft and Soluk 2005).

Broadly applicable patterns in the strength of multiple predator effects may be recognized most easily by examining the influence of factors which are common to most ecological systems. Intraguild predation is one factor that is present in most systems (Arim and Marquet 2004), and has a strong influence on multiple predator effects (Finke and Denno 2002, Crumrine and Crowley 2003, Lang 2003, Warfe and Barmuta 2004). However, intraguild predation may itself be variable across environments, depending on the quality of prey refuges that decrease the efficiency of predator foraging (Gause 1934, Huffaker 1958, Jackson et al. 2001, Byers 2002, Grabowski 2004). Variable strengths of intraguild predation may thus lead to habitat specific strengths of risk reduction.

A second factor that is common to all systems is variation in the density of interacting species. Species density has the potential to strongly influence the effects of multiple predator species, as prey density will influence the intensity of competitive interactions for a shared resource and predator density will influence the frequency of interactions among predators. While previous studies have documented changes in multiple predator effects with changes in prey density (Soluk 1993, Losey and Denno 1998, Vance-Chalcraft and Soluk 2005), none have examined multiple predator effects at different predator densities.

The densities of *C. maenas* and *H. sanguineus* are highly variable, depending on habitat type and prey availability. Further, strong aggressive interactions between and among these species leads to intraguild predation and cannibalism when size differences

between interacting individuals are large (Lohrer and Whitlatch 2002a). Interactions between these species thus provide an excellent opportunity to examine patterns in multiple predator effects resulting from changes in predator and prey density and due to the variable presence and strength of intraguild predation.

I use a series of field and laboratory experiments to examine how intraguild predation and species density influence multiple predator effects among *C. maenas* and *H. sanguineus*. In Chapters 1 and 2 I examine the importance of intraguild predation for multiple predator effects using juvenile and small adult crabs of both species. I show that multiple predator effects become stronger with increased threat of intraguild predation. I then demonstrate that the strength of multiple predator effects varies with changes in prey density (Chapter 3), and predator density (Chapter 4). Finally, in Chapter 5 I explore the impacts of these interactions for freely foraging crabs across several sites in the Gulf of Maine. Together these studies demonstrate that interactions between *C. maenas* and *H. sanguineus* greatly influence predation by *C. maenas*, but not by *H. sanguineus*.

Species Redundancy

Species that perform similar functions within a community are sometimes grouped together into functional guilds that are followed as single units without regards to individual species within the guild. This approach is often taken as a step to simplify community dynamics. For example, many ecosystem simulation models lump species together into functional groups (e.g., Ecopath). This approach may most appropriately be applied when the impacts of different species are functionally equivalent, or redundant, meaning they can be readily substituted without changing ecological or community

processes (Lawton and Brown 1993). However, species can differ in myriad ways, and similarity of ecological function, or redundancy, is thus a multifaceted concept (Loreau 2004). Lumping similar species may therefore oversimplify complex systems, compromising the utility of the guild approach (Polis 1991, Polis and Strong 1996). Yet if species are shown to be redundant in certain ecological functions that define their roles in natural communities (e.g., similar prey consumption by different predator species), then the use of the guild approach may be warranted despite differences in other factors.

The majority of studies examining redundancy of multiple predator species have compared per capita impacts of single individuals or equal densities of individuals that were demographically similar (same size, sex, etc.) (e.g., Harris 1995, Kurzava and Morin 1998, Chalcraft and Resetarits 2003b, Chalcraft and Resetarits 2003a). Yet individual predators are rarely isolated in their impacts on natural systems, and interactions between both conspecifics and heterospecifics can influence per capita impacts (e.g., Peckarsky 1991, Eklöv and Werner 2000, Mistri 2003). Further, the level of understanding needed to assess the redundancy of invading species on native communities is at the population level. That is, the questions of interest are typically: what are the impacts of a new invasive species population on the native community and how do these impacts differ from those of populations of species already present?

To fully understand the redundancy of different species, we therefore need to assess how their impacts are influenced by interactions with other species (Sih et al. 1998) and how they are influenced by interactions within diverse populations that may be at differing densities. The invasions of *C. maenas* and *H. sanguineus* again provide an excellent opportunity to address these issues. Previous studies have documented

similarities and differences in resource use by these species in an attempt to compare their impacts on invaded prey communities (Tyrrell and Harris 1999, Lohrer et al. 2000, DeGraaf and Tyrrell 2004, Tyrrell et al. 2006). However, aggressive interference is strong both within (Smallegange et al. 2006) and between these species (Jensen et al. 2002, Lohrer and Whitlatch 2002a). Further, population densities and sizes of individuals of these two species are vastly different (Lohrer and Whitlatch 2002b, a). Redundancy in per capita effects may therefore depend on the strength of aggressive interactions that likely depend on relative predator size and species (Chapter 1). And redundancy in the population level effects may likely depend on population densities and interactions with conspecifics and heterospecifics.

In Chapter 6 I use a field enclosure experiment to compare population level effects of the two crab species at a range of predator densities on the broad prey community in order to determine whether population level effects of the two predators are redundant. In a second experiment I also examine how interactions between the species influence their impacts on the prey community. Because the two experiments were conducted in different years when differences existed in the prey community, I compared redundancy across years to determine whether redundancy is determined at least in part by supply side dynamics. Additionally, both experiments were conducted over the duration of the entire "foraging season" and include both direct predatory as well as density and trait mediated indirect effects.

CHAPTER 1

INTRAGUILD PREDATION REDUCES REDUNDANCY OF PREDATOR SPECIES IN MULTIPLE PREDATOR ASSEMBLAGE

Abstract

Interference between predator species frequently decreases predation rates, lowering the risk of predation for shared prey. However, such interference can also occur between conspecific predators. Therefore, to understand the importance of predator biodiversity and the degree that predator species can be considered functionally interchangeable, we determined the degree of additivity and redundancy of predators in multiple- and single-species combinations. We show that interference between two invasive species of predatory crabs, *Carcinus maenas* and *Hemigrapsus sanguineus*, reduced the risk of predation for shared amphipod prey, and had redundant per capita effects in most multiple- and single-species predator combinations. However, when predator combinations with the potential for intraguild predation were examined, predator interference increased and predator redundancy decreased. Our study indicates that trophic structure is important in determining how the effects of predator species combine and demonstrates the utility of determining the redundancy, as well as the additivity, of multiple predator species.

Introduction

Species that perform similar functions within a community are sometimes grouped together into functional guilds that are followed as single units without regards to individual species within the guild (e.g., aquatic invertebrates: Cummins 1973, amphibians and reptiles: Inger and Colwell 1977, stream fish: Winemiller and Pianka 1990, marine fish: Greenstreet 1996). This approach is often taken as a step to simplify community dynamics. For example, many ecosystem simulation models lump species together into functional groups (e.g., Ecopath). This approach may most appropriately be applied when the impacts of different species are functionally equivalent, or redundant, meaning they can be readily substituted without changing ecological or community processes (Lawton and Brown 1993).

The utility of the guild approach has been questioned due to potential oversimplification of complex systems (Polis and Strong 1996). As an example of this complexity, interactions between members of predator guilds often do not result in additive combined predation (Sih et al. 1998). Rather, interactions between predator species that share a common prey often yield less than additive predation (risk reduction, e.g., Eklöv 2000, Eklöv and Werner 2000, Finke and Denno 2002, Crumrine and Crowley 2003, Lang 2003, Warfe and Barmuta 2004), or sometimes, greater than additive predation (risk enhancement, e.g., Losey and Denno 1998, White and Eigenbrode 2000, Eklov and VanKooten 2001, Cardinale et al. 2003, DeWitt and Langerhans 2003, Meyer and Byers 2005).

However, the presence of nonadditive impacts of multiple predators need not automatically preclude use of a predator guild approach. While nonadditivity may occur

when multiple predator individuals are combined, this may be independent of the identity of the predator species, i.e., whether conspecifics or heterospecifics are combined. For instance, interference between predator species can decrease predation rates of one or both species, causing risk reduction (e.g., see Chapter 2 and Eklöv and Werner 2000, Warfe and Barmuta 2004). However, interference between predators of the *same* species can also cause predators to decrease their rates of prey consumption (Mansour and Lipcius 1991, Clark et al. 1999). Previous studies have shown that such interference between conspecific and heterospecific predators may not only be non-additive, but may also be redundant (Peckarsky 1991), leading to similar levels of risk reduction for shared prey (see Chapter 3 and Vance-Chalcraft et al. 2004, Vance-Chalcraft and Soluk 2005a). We will refer here to this aspect of redundancy as redundancy in the interference effects of predators.

In addition to redundant interference effects between predators, prey consumption by predator combinations may also be redundant. That is, heterospecific predator combinations often cause similar levels of prey mortality as conspecific predator combinations (White and Eigenbrode 2000, Schmitz and Sokol-Hessner 2002, Sokol-Hessner and Schmitz 2002), indicating that predators are substitutable (*sensu* Sih et al. 1998). We will refer here to this aspect of redundancy as redundancy in the trophic effect of predators.

While previous studies have examined either the interference or the trophic effect, we believe that examining both effects of predators together may provide a more complete assessment of the redundancy of predators than examining only one or the other. Understanding these different facets of multispecies predator-prey interactions

will provide insight into the dynamics of natural communities, will inform the extent to which predator biodiversity is important for ecosystem functioning in the face of rapid changes in biodiversity resulting from species/habitat loss and biological invasion (Ruesink and Srivastava 2001, Kinzig et al. 2002, Ives et al. 2005), and will more comprehensively inform the extent to which a predator guild approach may be applied in determining the impacts of predators on prey populations.

Determining whether multiple predator species are additive and/or redundant may, however, be complicated by processes and interactions that occur other than consumption of a shared prey. One interaction that often influences the effects of multiple predators is intraguild predation (see Chapter 2 and Polis et al. 1989, Rosenheim 1998, Finke and Denno 2002, Crumrine and Crowley 2003, Lang 2003, Rosenheim and Corbett 2003, Warfe and Barmuta 2004). Intraguild predation (IGP) occurs when competing predators also consume each other (Polis et al. 1989), and can result in both density indirect effects and trait mediated indirect effects on prey (Werner and Peacor 2003). (We use the term IGP here to include cannibalism). IGP often occurs only between certain life history stages, such as adults preying on juveniles (reviewed in Polis et al. 1989). Interactions between predator species in the field may thus be highly variable when multiple sizes of individuals of the two species overlap, leading to the potential for IGP in some interactions and not in others. Thus it may be necessary to determine the additivity and redundancy of many pair-wise interactions of different sized predators to fully understand how multiple predator species combine to affect shared prey. To examine these issues of redundancy, we examined predation by two invasive species of intertidal crab predators that share the same prey resources.

Natural History

Two invasive predatory crabs are predominant on New England shores, the European green crab *Carcinus maenas* (Linnaeus, 1758) and the Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835). *C. maenas* invaded the east coast of North America in the mid 1800's and subsequently spread from Maryland to Nova Scotia. *H. sanguineus* was introduced around New Jersey in 1988 and has quickly spread over much of the same region from North Carolina to central Maine. In the Gulf of Maine, multiple sizes of these predators share the same intertidal distribution and are often found under the same rocks (see Chapter 2). Intraguild predation occurs among these species, with larger individuals of each species consuming smaller heterospecific and conspecific individuals (Lohrer and Whitlatch 2002). We could thus control whether IGP was possible by manipulating the sizes of predators in experimental treatments. Encounters between different sized individuals of the two species are frequent due to their overlapping distribution. Thus, operationally we must understand whether combinations of different sizes of the two predators are additive and/or redundant to better understand the combined impacts of these predators on prey resources.

Previous work has shown that these generalist predators have similar diets (Tyrrell and Harris 1999, Lohrer et al. 2000, Griffen unpubl. data) and that they interfere with each other while competing for the same food resources (Jensen et al. 2002). Gammarid amphipods are an abundant prey source in areas where these predators are found together. For example, at Odiorne Point, NH, a semi-exposed site where both crabs are found abundantly (see Chapters 2 and 5), amphipods are present in the mid intertidal in patchily high densities (368 ± 390 m^{-2}, avg. $\pm$ SD, $n = 21$; Griffen unpubl.

data). Further, amphipods are a common prey for both crab species. McDermott (1998) found amphipods in the guts of 22% of *H. sanguineus,* and our own analyses indicate that 10-20% of the diet of *C. maenas* is composed of amphipods (Griffen, unpubl. data). Thus, using *C. maenas* and *H. sanguineus* as predators of shared amphipod prey provided a realistic, experimentally tractable predator-prey system that allowed us to assess redundancy of multiple predators with and without IGP.

In a laboratory experiment, we addressed the following questions: First, do isolated *C. maenas* and *H. sanguineus* have similar per capita predation rates when foraging on amphipods (i.e., are they redundant in their effects on prey)? Second, do isolated measurements of predation by each crab predator combine additively to predict prey consumption when both forage together? Or does interference between these species reduce predation risk for shared prey? Third, do interactions between heterospecific predators influence predation differently than interactions between conspecifics? And fourth, how are these comparisons influenced by IGP?

Methods

Experimental Design

We examined predation by *C. maenas* and *H. sanguineus* on amphipod prey in a laboratory experiment to isolate and quantify predator effects. We included 15 experimental treatments that combined all possible single and multiple species combinations of large and small predators (Table 1.1). Eight replicates of each treatment were used, with a single replicate of each treatment used during each of eight blocked, 24-h trials. Individual predators were only used in a single replicate.

We conducted the experiment in August 2004 in a controlled temperature/light room (temp = 20°C; light was a constant 16:8 h light:dark cycle, lux = 957). We filled 15 polypropylene containers (78 × 31.5 × 30 cm deep) with 1 cm of beach sand and 18 L (approximately 8 cm depth) of unfiltered seawater. Twelve denuded stones (7-10 cm diam) placed on top of the sediment created refuge habitat in each chamber. Sand, rocks, and seawater came from the New Hampshire coast. We changed seawater between trials and aerated continuously. Predators were starved for 24 h prior to experiments.

Large crabs of these species often prey on smaller individuals (Lohrer and Whitlatch 2002). Therefore, we created appropriate size differentials of individuals in our experiments to manipulate the potential for IGP and to control which of the two species was the top and intermediate predator (*H. sanguineus* – large: 2.11 ± 0.17 cm carapace width [CW] [avg. ± 1 SD], small: 1.35 ± 0.13 cm CW; *C. maenas* – large: 2.63 ± 0.18 cm CW, small: 1.33 ± 0.09 cm CW). We collected *C. maenas*, *H. sanguineus*, and amphipods (*Gammarus* spp.) by hand from Odiorne Point, NH. We conducted short experimental trials (24 h) using sufficient amphipod prey so that they were never limiting (50 in each treatment). This resulted in, at most, consumption of 50-60% of the prey available during each trial. Amphipod mortality was assessed at the end of each trial.

Combined prey consumption by multiple predator species may be altered by both IGP-related predator mortality (a density indirect effect), and by the threat of IGP that alters foraging behavior (a trait mediated indirect effect, see Chapter 2 and Crumrine and Crowley 2003). By using short term trials and an abundance of prey, we eliminated lethal IGP during our experiment. This was desirable because lethal IGP would have changed the overall density of predators and the presence/absence of intermediate

predators, potentially confounding interpretation of our results. We previously showed that behavioral components of IGP are an order of magnitude more influential to amphipod survival in this system than are direct losses of intermediate predators from IGP (see Chapter 2). Although short term experiments can heighten behavioral effects (Lima and Bednekoff 1999), the overriding influence of nonlethal (vs. lethal) IGP provided an ideal situation for examining the majority of the influence of IGP without its confounding influence on density.

Data Analysis

Individual Predation Rates. We first compared predation rates between the four types of predators (large and small individuals of each species) to determine whether they had redundant (i.e., equal) predation rates when foraging alone. We used a two-way ANOVA with each of the four predator types and the no predator control (treatments 1-4 and 15, Table 1.1) treated as separate levels of one factor and trial block as the second factor. This was followed by pair-wise comparisons at each of the levels of predator treatment (Tukey's, $\alpha = 0.05$). For all subsequent analyses described below, prey mortality in the no predator (control) treatment was subtracted from prey mortality in all other predator treatments within each trial before analyses to account for non-predatory mortality.

Predator Additivity. We determined whether predation by *C. maenas* and *H. sanguineus* foraging on amphipods was additive when the two species foraged together by comparing the proportion of prey consumed in each predator combination to values expected if the predators had additive effects. We determined expected (additive)

consumption of amphipod prey when both crab species foraged together using a multiplicative risk model (Soluk 1993) and prey consumption by single individuals of each predator type (i.e., Treatments 1-4, Table 1.1). Expected values were calculated independently for each multiple species predator combination and for each trial. We then determined whether the effects of the two predator species were additive using a three-way ANOVA on prey mortality with observed and expected predation as two levels of one factor (Vance-Chalcraft and Soluk 2005b), each heterospecific predator combination as different levels of a second factor (Treatments 9, 11, 12, and 14 in Table 1.1), and trial treated as a blocking factor. This was followed by planned linear contrasts ($\alpha = 0.05$) in which we directly compared observed and expected predation for each predator combination. A significant difference in a linear contrast indicates that predation by that predator combination is nonadditive. We chose this statistical approach because it has higher statistical power (degrees of freedom) than t-tests and individual 2-way ANOVAs performed on each predator combination—the methods typically used to detect nonadditive effects of multiple predators. We confirmed that this analysis yields qualitatively similar results to these other techniques.

Interference and Trophic Redundancy. We compared two aspects of the redundancy of *C. maenas* and *H. sanguineus* when multiple individuals foraged together: redundancy in the interference effects and in the trophic effects of these predators. We statistically examined each of these separately. We first examined redundancy in the interference effects of large individuals of each species. The magnitude of nonadditivity (observed minus expected prey consumption, see previous section) indicates the degree of interference or facilitation between conspecific or heterospecific predators. We

therefore used the multiplicative risk model (Soluk 1993) to calculate expected predation by conspecific predator pairs of each species (Vance-Chalcraft et al. 2004), and subtracted this from observed predation (Treatment 5-6, Table 1.1) to determine the magnitude of risk reduction. We then compared risk reduction when conspecific and heterospecific predators were paired to determine whether predator species identity was important in determining effects on other predators. We used two-way ANOVA on the magnitude of risk reduction with the three predator combinations (two large *C. maenas*, two large *H. sanguineus*, or one of each) as levels of one fixed factor, and trial block as the second factor. This was followed by Tukey's test for multiple comparisons between the three predator combinations. If no difference was found, this indicated that these predators were redundant in their interference effects on each other's predation. Identical analyses were conducted for combinations of small individuals to examine the interference redundancy of these predators.

We then examined the redundancy in the trophic effects of conspecific and heterospecific predator pairs using identical statistical analyses, but with prey mortality rather than risk reduction as the response variable.

When IGP was allowed by combining different sized predators, we analyzed each of the four conspecific and heterospecific predator combinations together (Treatments 10-13, Table 1.1). We again used a two-way ANOVA with the four predator combinations treated as separate levels of a fixed factor and trial block as a second factor, followed by Tukey's test for multiple comparisons. And we again conducted two analyses, one with risk reduction as the response variable (to assess the redundancy of the interference

effects of these predators) and one with prey mortality as the response variable (to assess the redundancy of the trophic effects of these predators).

We ensured that variances in the data for all ANOVAs were homoscedastic by examination of residual plots. Block effects were not significant in any of the analyses ($p > 0.15$). Although pooling the data by removing block from the analyses did not change the results, block was retained in all analyses for completeness (Hines 1996).

Results

Individual Predation Rates

Large and small crab predators of both species consumed amphipods in our experiments, but at different rates (ANOVA, $F_{4,39} = 60.49$, $p < 0.0001$). Thus the proportion of amphipod prey consumed differed between three of the four predators: Large *C. maenas* (0.41 ± 0.03) > large *H. sanguineus* (0.31 ± 0.03) > small *C. maenas* (0.16 ± 0.02) = small *H. sanguineus* (0.12 ± 0.02) > no predator control (0.04 ± 0.01).

Predator Additivity

Amphipod prey benefited from less than additive predation risk in the presence of some combinations of the two species, but predation by other combinations was additive (Fig. 1.1). Specifically, predation by large individuals of each species was less than additive (ANOVA with planned linear contrasts between observed and expected predation, $F_{1,49} = 8.44$, $p = 0.005$), as was predation when small *C. maenas* and large *H. sanguineus* were combined ($F_{1,49} = 18.52$, $p < 0.0001$). There was a marginally significant trend towards risk reduction when small individuals of both species were

combined, ($F_{1,49}$ = 2.99, p = 0.09). However, when large *C. maenas* and small *H. sanguineus* were combined predation was consistent with the prediction of the multiplicative risk model ($F_{1,49}$ = 0.03, p = 0.86).

Interference and Trophic Redundancy

We plotted predator interference effects and trophic effects together to facilitate comparison of the redundancy of the various predator combinations (Fig. 1.2). Redundant predator combinations in Fig. 1.2 cluster closely together. Large individuals interacting with other large conspecific and heterospecific predators were redundant in both their interference (ANOVA on risk reduction in heterospecific and conspecific predator combinations, $F_{2,23}$ = 0.57, p = 0.58; Fig. 1.2) and trophic effects (ANOVA on prey mortality caused by conspecific and heterospecific predator combinations, $F_{2,23}$ = 0.84, p = 0.45; Fig. 1.2). Similarly, small individuals of each species were redundant both in their interference effects on other predators ($F_{2,23}$ = 0.25, p = 0.78; Fig. 1.2) and in their trophic effects on prey mortality ($F_{2,23}$ = 0.56, p = 0.58; Fig. 1.2).

When IGP was allowed by combining different sized individuals of each species, there was a large, significant difference in interference effects, but only between treatments with different top predators (ANOVA followed by Tukey's test on risk reduction with all four predator combinations where IGP was possible, $F_{3,31}$ = 6.07, p = 0.004, Fig. 1.2). When the identity of the top predator did not change, risk reduction was similar in strength, whether large predators were paired with small conspecifics or with small heterospecifics (closed circles in Fig. 1.2 are similar to each other, and open circles in Fig. 1.2 are similar to each other). A similar pattern was observed when comparing the

trophic redundancy of these predator combinations (Fig. 1.2). Specifically, although there were no differences in amphipod consumption between treatments with the same top predator regardless of identity of intermediate predator, amphipod consumption was significantly higher when Carcinus was the top predator (ANOVA followed by Tukey's test on prey mortality, $F_{3,31} = 9.90$, $p < 0.001$, Fig. 1.2). No IGP-related predator mortality occurred during our experiment. Thus all effects were due to the threat of IGP rather than changes in predator density resulting from predator on predator mortality.

Discussion

Our study shows that when the threat of IGP is absent (i.e., when predators only interact competitively), *C. maenas* and *H. sanguineus* have redundant interference and trophic effects. Interference competition between these species has previously been observed. For example, *H. sanguineus* may frequently displace similar sized *C. maenas* when the two species directly compete for the same prey item, causing *C. maenas* to abandon captured prey (Jensen et al. 2002). Antagonistic interactions are also common among *C. maenas* (Griffen, pers obs), and can decrease predation rates (see Chapter 3 and 4). This conspecific interference is capable of altering foraging behavior to a similar extent as interactions with *H. sanguineus*, leading to redundant interference effects of these predators in the absence of IGP (Fig. 1.2).

However, the threat of IGP was high when large *H. sanguineus* were combined with small *C. maenas* (see below). In this case, combining the two species resulted in strong risk reduction for amphipods that was not redundant with *C. maenas* as the top predator (Fig. 1.2). Because the same species were used when IGP was and was not

possible, differences in results could be definitively attributed to changes in trophic structure, and were not confounded by a change in species. Thus, IGP may be an important factor in determining when interference between predator species causes reductions in predation risk for shared prey that cannot be predicted from single-species trials. This is consistent with a previous examination of several different species-combinations of stream predators that found risk reduction to be strongest when predators with the potential for IGP were combined (Vance-Chalcraft and Soluk 2005a), and with a previous study where we demonstrated that habitat-specific increases in consumption of *C. maenas* by *H. sanguineus* resulted in increased risk reduction for shared prey (see Chapter 2).

The degree of redundancy in the interference effect of these predators depended on the asymmetry of IGP. In a preliminary experiment, large *H. sanguineus* were much more likely to consume smaller heterospecifics than were *C. maenas*, and both species were more likely to consume heterospecifics than conspecifics (Griffen, unpubl. data). The threat of IGP can cause decreased predation by both top and intermediate predators as a result of changes in foraging behavior when the two forage together (Crumrine and Crowley 2003), and these behavioral changes are responsible for nearly 90% of the total risk reduction in this system (see Chapter 2). Changes in foraging behavior are often greatest when IGP is strong (Lima 1998), and thus were likely much stronger when *H. sanguineus* was the top predator than when *C. maenas* was the top predator and in heterospecific than conspecific predator combinations. Thus, strong IGP led to high risk reduction for shared prey (e.g., when large *H. sanguineus* was combined with small *C.*

maenas, Fig. 1.2), and asymmetry in IGP led to low redundancy (e.g., separation along both axes of Fig. 1.2 when *H. sanguineus* vs. when *C. maenas* was the top predator).

Our results have implications for determining the effects of *C. maenas* and *H. sanguineus* on amphipod prey populations. Interference between conspecifics and heterospecifics that decreases predation implies that multiple predator individuals should be included when determining the impacts of these predators on prey in order to avoid overestimation of population-level impacts. Further, redundancy in both the trophic and interference effects of these predators when individuals are the same size implies that these species can be combined to some extent into a single trophic guild when determining their impacts on some prey sources. This conclusion may also apply to other important prey for these predators, such as the mussel *Mytilus edulis* (Linnaeus, 1758). For example, similar sized *C. maenas* and *H. sanguineus* consume small mussels at similar rates (DeGraaf and Tyrrell 2004), and conspecific and heterospecific interference between these predators while foraging on mussels can reduce prey mortality by similar amounts (see Chapter 3). However, situations also likely occur where these two predators are not redundant because of diet shifts or different food preferences.

Some studies have reported only the trophic or only the interference effect of predator combinations (e.g., Sokol-Hessner and Schmitz 2002, Lang 2003, Vance-Chalcraft and Soluk 2005a). While these effects are not independent (trophic effects are observed prey mortality and interference effects are calculated using observed prey mortality), they do provide different information, and it therefore remains beneficial to examine both when determining the combined effects of multiple predators. For example, had we examined only the interference effect in our system, we may have

concluded that similar levels of interference provide equal safety for amphipods under different predator combinations. Similarly, had we examined only the trophic effect, we may have concluded that predation by various predator combinations caused either high or low prey mortality (Fig. 1.2). However, by examining both effects together it became apparent that some predator combinations with similar levels of interference differed in amphipod consumption by a factor of two, and that IGP is important in establishing levels of risk presented by different predator combinations (Fig. 1.2). Examining both of these effects together should lead to greater predictability of the effects of multiple predators.

We have demonstrated that the impacts of *C. maenas* and *H. sanguineus* vary in their additivity and redundancy. This variability became apparent by including two different factors in our study. First, examining both the interference and trophic effects allowed us to utilize these different components of the functional redundancy of these predators to more fully understand their interactions and combined effects (Fig. 1.2). Understanding the functional redundancy of species along multiple niche dimensions will be crucial to understanding the consequences of continuing changes in biodiversity in natural systems (Rosenfeld 2002). Second, we included different size combinations that incorporated the variable trophic complexity (presence or absence of IGP) that occurs between these species. The simultaneous presence of multiple sizes or life-history stages of predators often results in top and intermediate predators in natural systems (Polis et al. 1989) and, though not examined, occurs among many of the species for which the effects of multiple predators have been reported (e.g., McIntosh and Peckarsky 1999, Eklov and Werner 2000, Vance-Chalcraft et al. 2004). Our study implies that unique nonadditive

impacts of multiple predator species may be stage- or size-specific. The shifting redundancy of these species with trophic structure highlights the importance of IGP as a causative factor in non-redundant, non-additive effects of multiple predators. The population-level importance of predator species richness may therefore depend on IGP and the degree of interaction (e.g., encounter rates between different size classes), both of which are strongly dependent on population demographics.

Table 1.1 Predator treatments included in laboratory experiment to examine interference between *Carcinus maenas* and *Hemigrapsus sanguineus*. Abbreviations are as follows: large *C. maenas* (*CM*), small *C. maenas* (*cm*), large *H. sanguineus* (*HS*), and small *H. sanguineus* (*hs*). Numbers given are individuals per chamber. Fifty amphipods were used as prey in each of the 15 treatments. Each treatment was replicated eight times.

Treatment #	Predator(s)			
	CM	*HS*	*cm*	*hs*
1	1	–	–	–
2	–	1	–	–
3	–	–	1	–
4	–	–	–	1
5	2	–	–	–
6	–	2	–	–
7	–	–	2	–
8	–	–	–	2
9	1	1	–	–
10	1	–	1	–
11	1	–	–	1
12	–	1	1	–
13	–	1	–	1
14	–	–	1	1
15	Control: no predators, only amphipod prey			

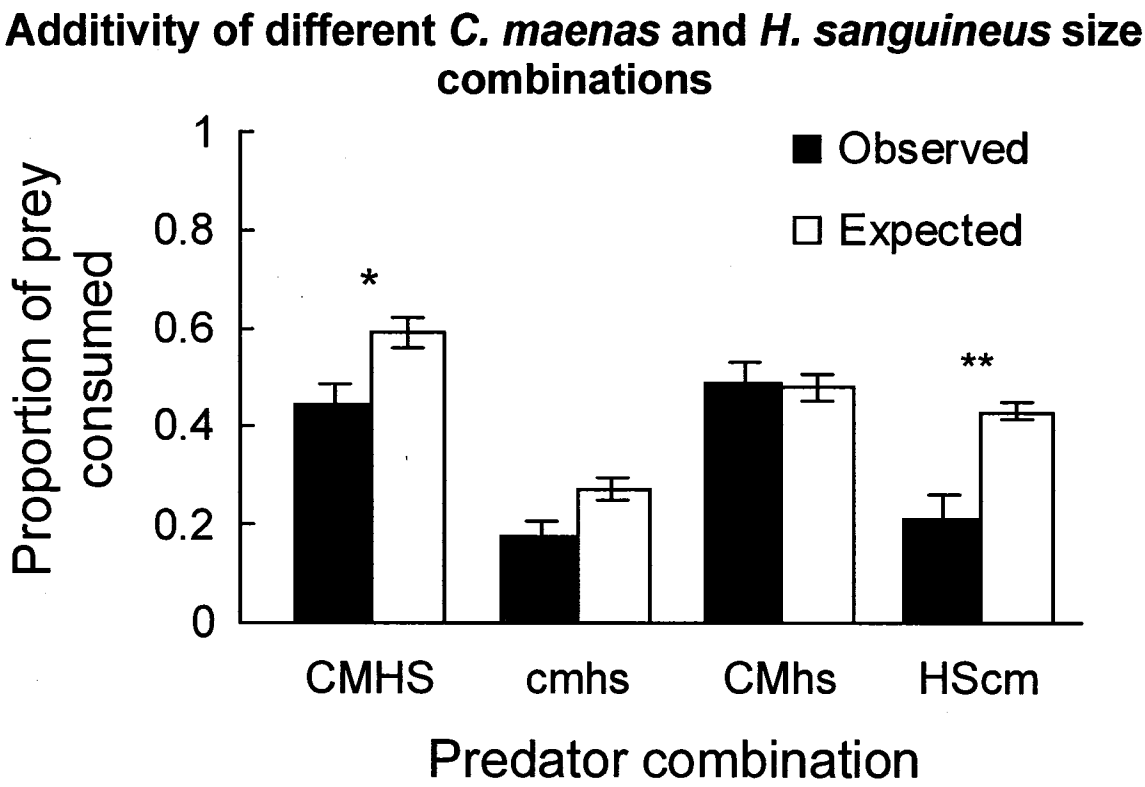

Figure 1.1 Observed and expected consumption of amphipods (mean ± 1 SE, n = 8) by *C. maenas* and *H. sanguineus* combined. Letters on the x-axis represent predators as indicated in Table 1 legend. Expected values indicate predation expected in the absence of interference and were derived from the multiplicative risk model (Soluk 1993). * $p < 0.01$, ** $p < 0.0001$, from ANOVA with paired linear contrasts.

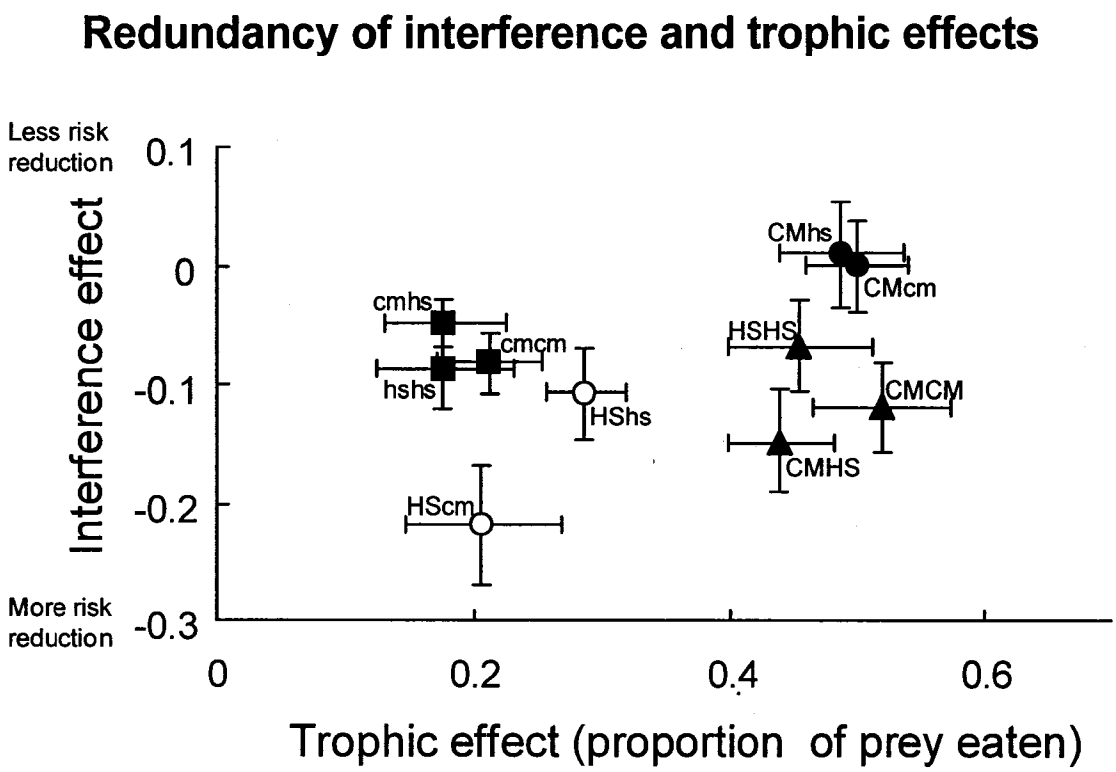

Figure 1.2 Functional niche of *C. maenas* and *H. sanguineus* illustrating both their interference effects on predation by conspecific and heterospecific predators and their trophic effects on shared prey (mean ± 1 SE, n = 8). Negative values represent stronger interference effects. Abbreviations next to each point are as given in Table 1. ▲ Are for combinations of large individuals. ■ Are for combinations of small individuals. ● (Both closed and open) Are for combinations of large and small individuals. All combinations of large individuals (▲) were similar in both their interference and trophic effects, as were all combinations of small individuals (■). Open and closed circles depict combinations of large and small predators that were different in their trophic effects (an identical pattern was observed in the interference effects, except that HShs treatment was not different from the CMcm and CMhs treatments; Tukey's, $\alpha = 0.05$).

CHAPTER 2

PARTITIONING MECHANISMS OF PREDATOR INTERFERENCE IN DIFFERENT HABITATS

Abstract

Prey are often consumed by multiple predator species. Predation rates on shared prey species measured in isolation often do not combine additively due to interference or facilitation among the predator species. Furthermore, the strength of predator interactions and resulting prey mortality may change with habitat type. We experimentally examined predation on amphipods in rock and algal habitats by two species of intertidal crabs, *Hemigrapsus sanguineus* (top predators) and *Carcinus maenas* (intermediate predators). Algae provided a safer habitat for amphipods when they were exposed to only a single predator species. When both predator species were present, mortality of amphipods was less than additive in both habitats. However, amphipod mortality was reduced more in rock than algal habitat because intermediate predators were less protected in rock habitat and were increasingly targeted by omnivorous top predators. We found that prey mortality in general was reduced by 1) altered foraging behavior of intermediate predators in the presence of top predators, 2) top predators switching to foraging on intermediate predators rather than shared prey, and 3) density reduction of intermediate predators. The relative importance of these three mechanisms was the same in both habitats; however, the magnitude of each was greater in rock

habitat. Our study demonstrates that the strength of specific mechanisms of interference between top and intermediate predators can be quantified but cautions that these results may be habitat specific.

Introduction

With few exceptions, prey are consumed by multiple predator species. The combined effect of multiple predators on shared prey is therefore an important component of community dynamics. Predation by multiple predators may be greater, or more frequently, less than predicted based on predation by each species separately (Sih et al. 1998). Shared prey consumption that is less than predicted, or risk reduction, often occurs when predators interfere with each other's foraging ability through processes such as intraguild predation (Crumrine and Crowley 2003, Lang 2003).

When intraguild predation occurs, interactions between top and intermediate predators (i.e., intraguild predators and intraguild prey, respectively) may reduce consumption of shared prey via three mechanisms: 1) decreased foraging by intermediate predators in the presence of top predators (behavioral effect); 2) decreased consumption of shared prey by top predators because they switch to foraging on intermediate predators (prey switching); and 3) decreased consumption of shared prey by intermediate predators because they themselves are consumed by top predators (density effect) (Crumrine and Crowley 2003). While these mechanisms are biologically distinct, they are closely associated and should often occur together.

The strength of these mechanisms may be habitat specific. For instance, prey refuges within habitats can decrease the efficiency of predator foraging (Gause 1934,

Huffaker 1958, Jackson et al. 2001, Byers 2002, Grabowski 2004), thus altering the intensity of interactions between predator and prey (Sietz et al. 2001, Woodley and Peterson 2003). Differential refuge value between habitats may therefore result in habitat specific foraging efficiency (e.g., Lipcius and Hines 1986). Additionally, habitat structures can reduce encounters between predators (Marshal and Rypstra 1999, Roda et al. 2000, Norton et al. 2001) and may therefore decrease interactions between predators (Grabowski and Powers 2004). Thus, changes in predator-prey and predator-predator interactions with habitat may lead to variable strengths of each of the mechanisms between habitats, resulting in habitat specific strengths of risk reduction. In fact, previous work has demonstrated that risk reduction can both increase (Warfe and Barmuta 2004) and decrease (Finke and Denno 2002) with changes in habitat complexity.

Differences in risk reduction for shared prey between habitats may be explained by differences in the strength of intraguild predation (i.e., differential risk of predation for intermediate predators between habitats). When intermediate predators are more vulnerable to predation, each of the mechanisms of risk reduction listed above may be stronger. For example, intermediate predators may alter foraging behavior in proportion to the threat of predation that they experience (Lima 1998). Thus the behavioral effect may be stronger when intermediate predators are more vulnerable to predation. Additionally, top predators may switch more readily from foraging on shared prey to foraging on intermediate predators in habitats where intermediate predators are more vulnerable to predation. This may lead to less shared prey consumption by both top predators and intermediate predators (i.e., stronger prey switching and density effect, respectively).

In a controlled laboratory experiment, we compared risk reduction for shared prey in two different habitat types that provided different levels of predation refuge to intermediate predators. We test the hypothesis that habitat specific changes in the strength of the mechanisms of risk reduction leads to stronger risk reduction in habitats where intermediate predators are more vulnerable. We show that risk reduction was greater in rock habitat where the risk of predation to intermediate predators was greater. Additionally, the strengths of each of the mechanisms responsible for reducing shared prey consumption were habitat specific, and were stronger in rock habitat.

Natural History

The relatively low species diversity found on marine rocky intertidal shores of New England provides an excellent opportunity to isolate interactions between a limited number of focal species. One such shore is found at Odiorne Point, a relatively sheltered site on the outer coast of New Hampshire, U.S.A. Two species of shore crabs are the dominant predators at Odiorne Point, the European green crab (*Carcinus maenas*) and the Asian shore crab (*Hemigrapsus sanguineus*). These two species have similar diets and potentially compete for food (Tyrrell and Harris 1999, Jensen et al. 2002). Additionally, predation occurs between these crabs, with larger individuals of each species consuming smaller heterospecifics (Lohrer and Whitlatch 2002). Low tide sampling at the site revealed that various sized individuals of the two species inhabited the same areas and were frequently found under the same rocks (Fig. 2.1). While various sized individual of both species were present, juvenile *C. maenas* and adult *H. sanguineus* were most frequently observed (Fig. 2.1).

The few potential prey sources found at the site include mussels (*Mytilus edulis*), snails (*Littorina littorea*), and amphipods (*Gammarus* spp.). Small *C. maenas* that predominate at Odiorne Point are inefficient at penetrating calcium carbonate shells of mussels and snails, but readily consume amphipods. Amphipods are also an important prey source for *H. sanguineus* (McDermott 1998, Lohrer et al. 2000),

The predominant refuge habitat for both crabs and amphipods at Odiorne Point is cobble, covering approximately 30% of the sandy substrate (Tyrrell and Harris 1999). Though spatially and temporally variable, drift algae is also common at Odiorne Point (Tyrrell and Harris 1999) and provides another important type of refuge habitat. *Ceramium rubrum* is a red alga that is a major component of the drift algae at Odiorne. We conducted mesocosms experiment in which we provided both rock and drift algae habitat to investigate the effects of these habitats on risk reduction.

Methods

Refuge Value of Habitats

We first determined the relative refuge from predation for intermediate predators provided by cobble and drift algae. Experimental mesocosms consisted of polypropylene containers (78 × 31.5 × 30 cm deep), containing 1 cm of beach sand and 18 L (approximately 8 cm depth) of unfiltered seawater. We provided refuge habitat using either 12 rocks (mean diameter approx. 10 cm) or 50 g wet weight of drift algae (*C. rubrum*) so that approximately 30% of the surface area of the mesocosms was covered by refuge habitat, thus facilitating comparison between habitat types with equivalent percent

cover. Sand, rock, algae, and water were obtained from the outer coast of New Hampshire, U.S.A.

We collected *H. sanguineus* and *C. maenas* by hand from Odiorne Point, NH, and placed them in separate aquaria without food for 24 h prior to experimentation to standardize hunger level. We used large *H. sanguineus* (carapace width [CW] = 2.16 ± 0.24 cm, mean ± SD) and small *C. maenas* (CW = 1.37 ± 0.10 cm) in the experiments because these sizes were the modal sizes for each species found at Odiorne Point, NH (Fig. 1), and the size differential was sufficient to elicit intraguild predation by the larger *H. sanguineus* on smaller *C. maenas* (Lohrer and Whitlatch 2002). We conducted experiments in a controlled temperature/light room in aerated seawater tanks at 20°C on a 16:8 light:dark cycle (lux = 957). Individual crabs were used only a single time.

We conducted five replicates in each habitat. We placed ten *C. maenas* in mesocosms containing either rocks or algae, followed by two large *H. sanguineus*. This *C. maenas* density is higher than the mean natural density (Fig. 2.1), however, it is within the range of natural densities observed in the field, and was necessary to give sufficient resolution for quantifying mortality due to *H. sanguineus* predation. Mortality of *C. maenas* was assessed after 24 h and was compared between the two habitats using a two-tailed t-test.

Risk Reduction in Each Habitat

We examined the relative strength of risk reduction in algal and rock habitats by conducting multiple predator experiments in each habitat type. We established experimental mesocosms and refuge habitats as described above for the habitat refuge

experiment. Fifty amphipods (0.5-1 cm total length) were added to each mesocosm 1 h before the addition of one *H. sanguineus*, three *C. maenas*, or no predators (control). These crab densities fall within the natural densities observed at Odiorne Point, NH (Fig. 1). Amphipod densities at Odiorne Point are extremely variable, ranging from none to thousands m^{-2}. We therefore chose the experimental amphipod density to ensure that amphipods were not completely depleted during the course of the trials.

The experiment included seven predator treatments in each of the two habitat types (Table 2.1) to quantify their effect on shared prey (amphipod) mortality. In three of these treatments, predators were rendered nonlethal by removing chelipeds and gluing the maxillipeds with cyanoacrylate. Based on extensive preliminary studies, both procedures were necessary to prevent crabs from killing or consuming amphipods. Neither of these procedures appeared to affect crab foraging behavior, as nonlethal crabs still attempted to capture prey. We conducted six 48-h trials with a complete treatment combination replicated once during each trial. For each trial, we randomized treatments among mesocosms and changed water in experimental mesocosms.

The presence of risk reduction within each habitat type was determined by comparing observed amphipod mortality when predators foraged together (i.e., when predator interference potentially occurred) to predicted prey consumption if predators had additive effects. Predicted prey consumption when the predators were combined was derived from predation by each species separately using the multiplicative risk model (Soluk 1993). Specifically, predicted prey consumption (C_{HC}) was calculated as follows:

$$C_{HC} = N(P_H + P_C - P_H P_C) \qquad (2.1)$$

where N is the number of prey at the start of the experiment, and P_H and P_C are the probability of prey consumption by *H. sanguineus* and *C. maenas* alone, respectively. The $P_H P_C$ term accounts for the fact that as prey are consumed they are no longer available to other predators. C_{HC} was calculated independently for both habitat types in each trial. Differences between the model predictions and observed predation when both predator species were combined indicate either risk reduction or risk enhancement. Risk reduction resulting from predator interference was anticipated because of antagonistic interactions between *H. sanguineus* and *C. maenas* (Lohrer and Whitlatch 2002). Therefore, observed and predicted (C_{HC}) amphipod mortality were compared within each habitat type using one-tailed, paired *t*-tests to determine whether predators had additive effects (Swisher et al. 1998, Warfe and Barmuta 2004).

Partitioning Risk Reduction

The importance of each of the three mechanisms that reduce shared prey mortality was determined using the nonlethal predator treatments (Table 2.1) and was calculated for each trial separately, as follows (adapted from Crumrine and Crowley 2003):

Behavioral Effect. Shared prey mortality is reduced as intermediate predators alter their foraging behavior in the presence of top predators. We quantified this reduction in amphipod mortality by subtracting shared prey consumption when intermediate predators foraged in the presence of a nonlethal top predator (Table 2.1, treatment 4) from prey consumption when intermediate predators foraged alone (Table 2.1, treatment 2).

Prey Switching. Shared prey mortality is reduced as top predators forage on intermediate predators rather than on amphipods. We quantified this reduction in amphipod mortality by subtracting shared prey consumption when top predators forage in the presence of nonlethal intermediate predators (Table 2.1, treatment 5) from prey consumption when top predators foraged alone (Table 2.1, treatment 1).

Density Effect. To calculate the density effect one must know the number of intermediate predators that die and thus how many shared prey survive as a direct result of having fewer predators. Treatment 3 (Table 2.1) determined the number of intermediate predators (*C. maenas*) that died as a result of combining lethal top and intermediate predators. To address the second component of the density effect, we conducted a second, separate experiment in which we measured the number of amphipods consumed by one, two, and three *C. maenas* in the presence of nonlethal *H. sanguineus*. This complete suite of densities allows us to account for potential nonlinearities in our calculation of the density effect if conspecific interference among intermediate predators occurs. We included nonlethal *H. sanguineus* to account for reduced foraging by *C. maenas* due to the presence of *H. sanguineus* (i.e., the behavioral effect) and thus avoid overestimating predation by *C. maenas* in our calculation of the density effect. The difference between amphipod consumption by three and two *C. maenas*, and by three and one *C. maenas*, indicates the impact of decreasing the intermediate predator density by one and by two, respectively. The reduction of live *C. maenas* quantified in each replicate of Treatment 3 could thus be translated into the number of amphipods that would have been consumed if *C. maenas* had not died.

As described, the calculation to this point yields a maximum density effect estimate that would occur if the death of intermediate predator *C. maenas* occurred immediately. However, the exact time that intermediate predators were consumed during the trials was unknown, and some may have eaten amphipods before dying. We therefore assumed that *C. maenas* died at the midpoint of each trial, and thus divided this maximum reduction in amphipod mortality in each trial by two. Other assumptions regarding the timing of *C. maenas* mortality did not change the conclusions drawn about the influence of the density effect.

We compared the strength of risk reduction and the contribution of each of the mechanisms in each habitat using a two-way ANOVA with reduction in amphipod consumption (i.e., risk reduction) as the response variable and mechanism (three levels) and habitat (two levels) as fixed factors. We transformed the data [ln(x+1)] prior to analysis to meet the assumptions of ANOVA.

Results

Refuge Value of Habitats

The experiment that compared the relative refuge from predation for intermediate predator *C. maenas* between habitats indicated that rock was the riskier habitat, as *C. maenas* mortality in the rock habitat was 2.5 times that in the algal habitat (two-tailed *t*-test, $t = 2.27$, $df = 8$, $p = 0.028$, Fig. 2.2). Based on this result, if risk reduction for amphipods occurs, it is expected to be stronger in rock than in algal habitats.

Risk Reduction in Each Habitat

Each predator consumed amphipods when foraging separately in both habitats, and *C. maenas* consumed more amphipods than did *H. sanguineus* (Fig. 2.3). When both predators foraged together, amphipod mortality was lower than predicted based on predation by each species separately, indicating that risk reduction occurred in both rock and algal habitats. Specifically, the proportional reduction in amphipod mortality was 0.38 ± 0.06 (avg. ± SE) in rock and 0.20 ± 0.05 in algae (one-tailed, *t*-tests, $t = 3.77$, df = 5, $p = 0.006$ and $t = 6.75$, df = 5, $p = 0.0005$, respectively; Fig. 2.3).

Partitioning Risk Reduction

The behavioral effect, prey switching, and density effect all contributed to risk reduction in both of the habitat types (Fig. 2.4). Each was stronger in rock than in algae, leading to stronger risk reduction in rock than in the algal habitat (ANOVA habitat effect: $F_{1,35} = 5.83$, $p = 0.022$; Fig. 2.4). The mechanisms of predator interference differed in their effects on risk reduction (ANOVA mechanism effect: $F_{2,35} = 7.48$, $p = 0.002$; Fig. 2.4). However, the relative effects of the mechanisms did not vary significantly between habitats (ANOVA habitat × mechanism interaction: $F_{2,35} = 0.40$, $p = 0.67$; Fig. 2.4). The behavioral effect (reduced foraging by *C. maenas* in the presence of *H. sanguineus*) was the largest; it was responsible for 67% of the reduction in amphipod mortality in the algal habitat and 48% in the rock habitat. Prey switching (reduced consumption of amphipods by *H. sanguineus* as it forages instead on *C. maenas*) decreased amphipod mortality more in rock (38%) than in algal habitats (21%). The density effect (decreased number of

intermediate predators available to consume shared prey) was similar in both habitats at 14% in rock and 12% in algae.

Discussion

We have shown that the strength of interference between predator species is habitat specific (Fig. 2.4) and that the relative magnitude of risk reduction in different habitats can be readily quantified and partitioned into its underlying mechanisms. While prey switching and density effect occurred in both habitats, the behavioral effect accounted for most risk reduction in both habitats, indicating that *C. maenas* reduced its feeding when *H. sanguineus* was present, regardless of the habitat. Even though the chance of predation was greatly reduced for *C. maenas* in algae compared to rock (Fig. 2.2), the behavioral effect was still strong in this habitat. Strong behavioral effects can still occur in habitats where intermediate predators are relatively more protected from top predators, if intermediate predators are incapable of discerning predation risk from top predators (Grabowski 2004).

The behavioral and prey switching effects examined here are examples of trait-mediated indirect interactions. Specifically, the behavioral effect is mediated by changes in intermediate predator foraging behavior, and prey switching is mediated by changes in top predator foraging behavior. In contrast, the density effect is a density-mediated indirect interaction. Few studies have attempted to partition the relative importance of these two components of indirect effects (reviewed in Werner and Peacor 2003), and their relative importance across different habitat types remains uncertain. While we found that the total indirect effect (i.e., risk reduction) was stronger in the rock than in the algal

habitat, there was little difference in the relative importance of trait- and density-mediated effects across habitat types. Trait-mediated effects were responsible for 88% and 86% of the total risk reduction in algal and rock habitats, respectively, with the density effect accounting for the remainder (Fig. 2.4). These findings are consistent with previous arguments that behavioral, or trait-mediated indirect interactions of predators may be stronger than density-mediated indirect interactions (Werner and Peacor 2003).

Our results are also consistent with previous studies that have shown the strength of risk reduction to be habitat specific (Finke and Denno 2002, Warfe and Barmuta 2004). Differences in risk reduction between the habitats in our study resulted from increased strength of each of the mechanisms in rock as compared to algae (Fig. 2.4). This was anticipated because *C. maenas* was more vulnerable in rock than in algae (Fig. 2.2). Thus, the difference in vulnerability of *C. maenas* between the two habitats was directly responsible for the difference in risk reduction. Our study therefore shows that when top and intermediate predators are present, the difference in risk reduction between habitats may be explained by differential refuge value of each habitat for intermediate predators. The riskiness of rock habitat for *C. maenas* is consistent with patterns of habitat use by *C. maenas* in the presence of *H. sanguineus* (Jensen et al 2002). Jensen et al. (2002) demonstrated that the number of juvenile *C. maenas* found under rocks is drastically reduced in the presence of *H. sanguineus*, as compared to areas where the two species do not overlap, i.e. the coast of central/northern Maine.

Changes in shared prey behavior in response to predator presence can also cause multiple predators to have nonadditive predation (Losey and Denno 1998, Eklov and VanKooten 2001, Harvey et al. 2004). Thus habitats that cause or allow prey species to

behave differently could also be responsible for differences in nonadditive effects of predators between habitats. However, preliminary observations in our system indicate that while amphipods increased refuge use in the presence of predators, this did not depend on predator identity or refuge type (Griffen, unpubl. data). Differences in risk reduction between rock and algal habitats were thus most strongly affected by changes in predator foraging behavior. Other factors, such as prey density, may also influence the magnitude of risk reduction. Amphipod density in the field is highly variable, and previous work has shown that the magnitude of risk reduction or risk enhancement may (Soluk 1993, Losey and Denno 1998) or may not (Vance-Chalcraft and Soluk 2005) change with prey density.

Nonlethal predators in our experiments were rendered nonlethal by the only method that proved to successfully reduce predation, removal of their chelipeds. However, this manipulation may have simultaneously decreased the defensive capabilities of intermediate *C. maenas* predators, as more nonlethal than lethal *C. maenas* predators were consumed by *H. sanguineus* in each habitat type during our experiment. The treatment where lethal top predators and nonlethal intermediate predators were combined (treatment #5, Table 2.1) may therefore overestimate the magnitude of prey switching observed in this experiment. Because overall risk reduction is the total of the behavioral, prey switching, and density effects, we could independently calculate the prey switching effect by subtracting the density and behavioral effects from the overall risk reduction in each habitat (treatment #3, Table 2.1). This calculation produced a virtually identical estimate of prey switching to our experimental estimate and therefore did not change the relative importance of the various mechanisms in each habitat.

Most natural environments are not homogeneous, but rather, are a mosaic of habitat types that provide varying levels of refuge for prey species. We have shown that differences in refuge value between habitats can lead to behaviorally-mediated changes in trophic interaction in multiple predator systems. Habitat specific changes in behavior can potentially link environmental heterogeneity to population and community dynamics through changes in refuge use and encounter rates among predators and between predators and prey (Chesson and Rosenzweig 1991). Understanding interactions between habitat use and behaviors that underlie complex trophic interactions may therefore lead to better predictions of population and community consequences of anthropogenic habitat change.

Table 2.1 Experimental treatments used to test for the presence of risk reduction when multiple predators foraged together and to determine the strength of the behavioral effect and prey switching. The strength of the density effect was calculated using data using additional data from a supplemental experiment as explained in the text. Each of these treatments was replicated six times in both rock and algal habitats. Numbers are individuals per mesocosm.

Treatment	**H. sanguineus**	**C. maenas**	Effect Tested
1	1	—	Predation rate of *H. sanguineus*
2	—	3	Predation rate of *C. maenas*
3	1	3	Presence and magnitude of risk reduction for shared prey when both predators forage together (Treatment 3 compared to model combination of Treatments 1 and 2)
4	1 Nonlethal	3	Changes in foraging behavior of *C. maenas* when *H. sanguineus* is present (Behavioral Effect, Treamtent 2 – Treatment 4)
5	1	3 Nonlethal	Reductions in foraging on amphipods by *H. sanguineus* due to prey switching to *C. maenas* (Prey Switching, Treatment 1 – Treatment 5)
6	1 Nonlethal	3 Nonlethal	Effectiveness of methods for rendering predators nonlethal
7	—	—	Background amphipod mortality

Density and size frequency distribution of *C. maenas* and *H. sanguineus* at Odiorne Point, NH

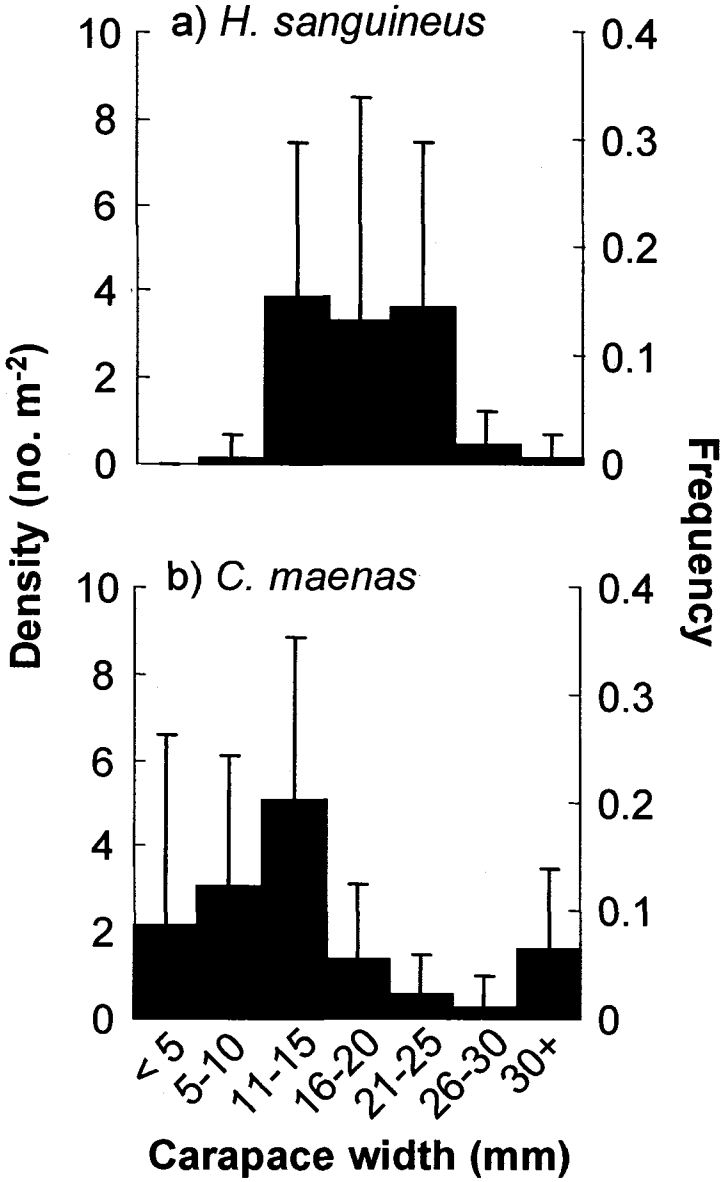

Figure 2.1 Density and frequency distribution (avg. + 1 SD) of carapace size classes for a) *H. sanguineus* and b) *C. maenas* at Odiorne Point, New Hampshire. Average was determined by sampling 0.5 m^2 quadrats (n = 15) at approximately 1 m above mean low water during low tide. The average density (± 1 SD) of all *C. maenas* and *H. sanguineus* at the site was 14 (± 8.9) and 11.4 (± 7.9) ind. m^{-2}, respectively

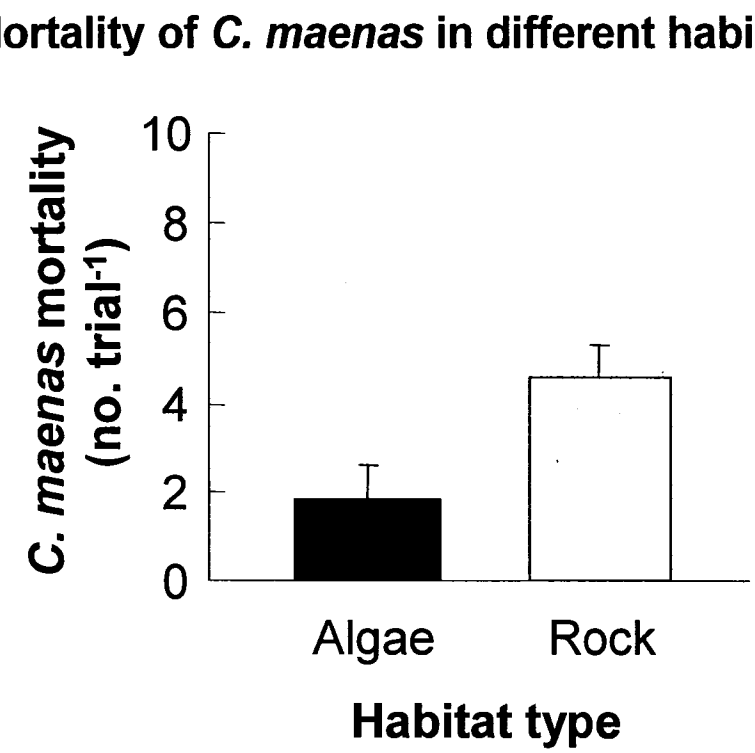

Figure 2.2 *C. maenas* mortality (avg. + SE, n = 5) due to predation by *H. sanguineus* in algal (*C. rubrum*) and rock refuge habitats

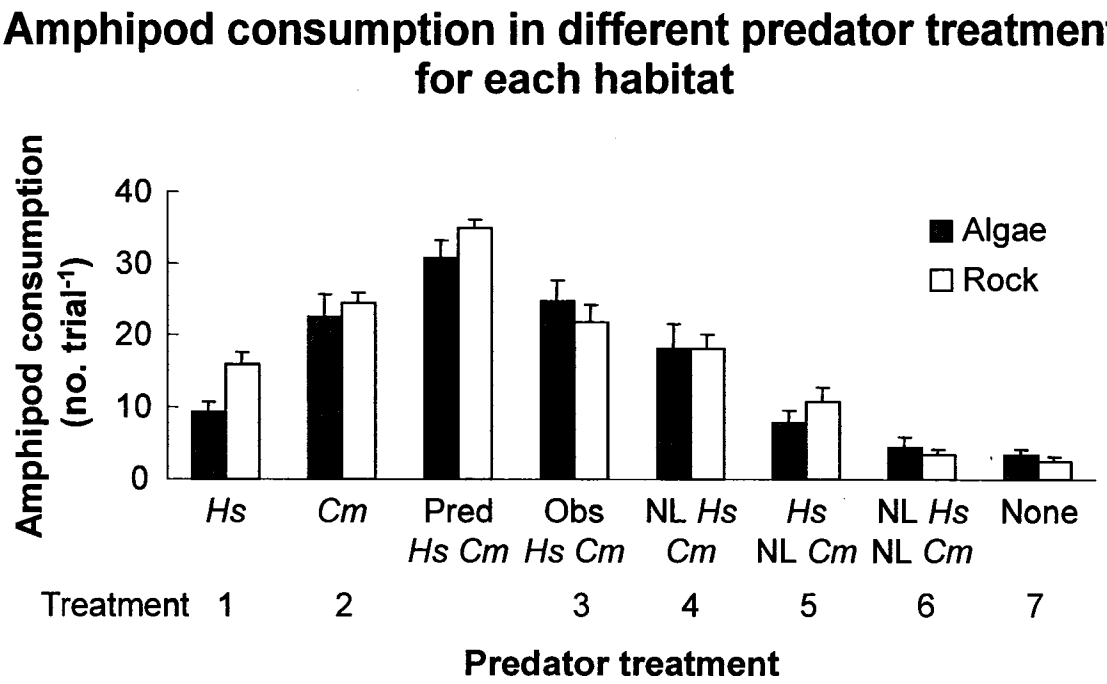

Figure 2.3 Consumption of shared prey (amphipods) (mean + SE, n = 6) in algal (*C. rubrum*) and rock habitats in predator treatments: top predator *H. sanguineus* (*Hs*), intermediate predator *C. maenas* (*Cm*), predicted consumption by both predators together based on single predator treatments (Pred *Hs Cm*), observed consumption by both predators together (Obs *Hs Cm*), combinations with nonlethal predators (NL) and no predators (None). Numbers on x-axis correspond to the treatment number shown in Table 2.1

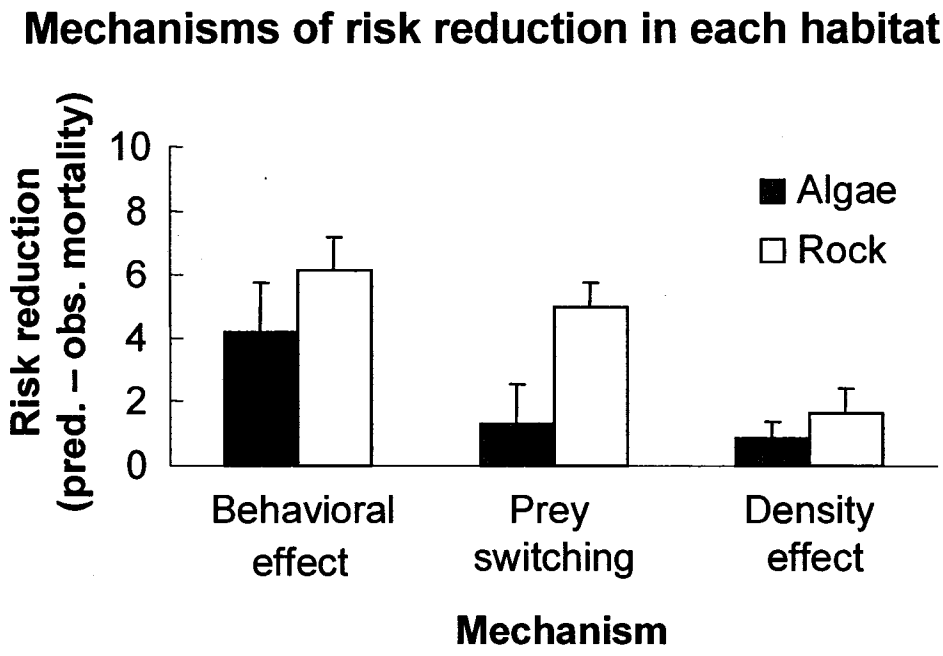

Figure 2.4 Magnitude of risk reduction (mean + SE, n = 6) for shared amphipod prey attributable to behavioral effect, prey switching, or density effect mechanisms in algal (*C. rubrum*) and rock habitats. Magnitude of risk reduction was determined by the difference between predicted and observed prey mortality in each habitat type, respectively

CHAPTER 3

DETECTING EMERGENT EFFECTS OF MULTIPLE PREDATOR SPECIES

Abstract

When foraging together, multiple predator species that share a single prey often cause prey mortality that cannot be predicted based on knowledge of predation by each species separately. Modeling and managing the effects of multiple predator species depends on accurately assessing these combined effects. Two methods are currently used to experimentally examine combined predation by multiple predator species: the additive and substitutive experimental designs. I simultaneously employed both experimental designs to examine predation by two crab species on shared mussel prey. I show that the two methods yield results that disagree both quantitatively and qualitatively, leading to very different conclusions about the way that predator species combine to affect prey mortality. This discrepancy occurred because the two methods examine complimentary, but not interchangeable questions. I advocate using an experimental design that incorporates both additive and substitutive designs to achieve a more complete understanding of the combined effects of multiple predator species.

Introduction

Much of the early empirical and theoretical work on predator-prey interactions involved only a single species of predator. However, in reality most prey are subject to

consumption by multiple predator species. This awareness has led to considerable attention over the last decade on the combined effects of multiple predator species on shared prey. Predation by multiple species often does not combine additively, rather predation is often greater (risk enhancement) or less (risk reduction) than additive. Both of these impacts are broadly termed emergent multiple predators effects (Sih et al. 1998), because they cannot be predicted based on knowledge of predation by each species separately. However, nonadditive predation can also occur when multiple predators of the same species forage together (Beddington 1975, Hassel 1978). Thus effects of multiple predator species are only truly emergent if the degree of nonadditivity is different than that resulting from interactions between conspecific predators (Sih et al. 1998, Vance-Chalcraft et al. 2004).

Emergent effects of multiple predator species can have important ecological and economic implications. For example, the effects of predator species may combine synergistically to limit the expansion of nonindigenous prey (Harvey et al. 2004) or to suppress pest species in agroecosystems (Losey and Denno 1998) with subsequent positive effects on economically important crops (Cardinale et al. 2003). Alternatively, predator species may interfere with and/or consume each other, thus decreasing their combined effectiveness for controlling prey populations (Sih et al. 1985, Rosenheim 1998). The practical importance of emergent multiple predator effects to wider community dynamics illustrates the need to accurately detect their presence.

Two different experimental designs are commonly employed to detect risk reduction or risk enhancement: additive and substitutive (also referred to as replacement series) experimental designs. Both designs compare predation by each species separately

to predation when the species are combined. However, the two methods differ in the way that predator density and predator identity are manipulated. The more common additive experimental design establishes a set density for each predator species and maintains that density in both single-species and multiple-species treatments. By combining predators in this way, additive designs confound changes in the number of predator species present with changes in total predator density. These two factors can therefore not be disentangled to determine which has caused any resultant risk reduction or risk enhancement.

While less frequently used, the substitutive design is becoming more common (see Chapter 1 and Schmitz and Sokol-Hessner 2002, Sokol-Hessner and Schmitz 2002, DeWitt and Langerhans 2003, Siddon and Witman 2004, Vance-Chalcraft et al. 2004). Substitutive experiments hold total predator density constant while manipulating predator species richness. Total predator density and predator species richness are therefore not confounded in substitutive experiments. However, while total predator density remains constant, substitutive experiments have different relative densities of each species in single-species and multiple-species treatments. Thus substitutive experiments only examine the effects of interactions between species relative to effects of interactions between conspecifics.

These experimental designs are not only used in multiple predator studies, but have commonly been used to examine interspecific competition. Historically, substitutive designs have been used most extensively (Cousens 1991, Gibson et al. 1999). Yet the validity of this approach for assessing competition has been challenged, and the use of additive designs has been encouraged (reviewed in Snaydon 1991). Because these

designs address complimentary, but not identical hypotheses, the appropriate design depends on the question of interest. While the additive design asks whether nonadditive effects due to interspecific interactions occur at all, the substitutive design asks whether nonadditive effects due to interspecific interactions are as strong as those due to intraspecific interactions (Jollife 2000). Thus, the most comprehensive assessment of competition may be gained from a combination of the two designs, where the density of each competing species is varied independently (Snaydon 1991).

Similarly, it has been recommended that additive and substitutive designs be used in tandem for multiple predator studies to detect nonadditive effects and then to determine whether these effects arise from adding a second predator species or from increasing total predator density (Sih et al. 1998). Two studies published to date have followed this recommendation and have shown that nonadditive effects in multiple predator systems were duplicated with single-species predator pairs (Vance-Chalcraft et al. 2004, Vance-Chalcraft and Soluk 2005a), indicating that these effects were a consequence of changes in predator density rather than predator species richness. However, the majority of studies have frequently employed only the additive (e.g., Losey and Denno 1998, Eklöv and Werner 2000, Eklöv and VanKooten 2001, Finke and Denno 2002, Lang 2003, Warfe and Barmuta 2004) or only the substitutive (e.g., Schmitz and Sokol-Hessner 2002, Sokol-Hessner and Schmitz 2002, DeWitt and Langerhans 2003, Siddon and Witman 2004) design when testing for risk reduction and risk enhancement.

Under some conditions, the two experimental methods may yield the same results. However, because the two methods manipulate predator densities differently, they may yield different results whenever predator density is important in eliciting emergent

effects. For example, multiple predator species often interfere with each other, reducing predation rates and resulting in risk reduction for shared prey (see Chapters 1 and 2 and Peckarsky 1991, Soluk 1993, Eklöv 2000, Eklöv and Werner 2000, Warfe and Barmuta 2004). Similarly, conspecific predators also frequently interfere, thus reducing predation rates (Abrams and Ginzburg 2000). Because the substitutive design incorporates conspecific interference, while the additive design does not, results obtained using the two methods may disagree when conspecific interference occurs.

While the above discussion highlights the importance of predator density, studies using additive designs have also demonstrated that prey density can influence the strength of multiple predator effects (Soluk 1993, Losey and Denno 1998, Vance-Chalcraft and Soluk 2005b). However, the strength of interference among conspecific predators can also vary with prey density, similarly altering per capita predation (Arditi and Ginzburg 1989, Abrams and Ginzburg 2000). Because of the use of additive experiments, it is therefore uncertain whether reported changes in the magnitude of nonadditivity with changes in prey density are a unique outcome of the multiple predator system, or are similar to dynamics expected with a single predator species.

Here I compare multiple predator effects in a field experiment by simultaneously employing both an additive and substitutive designs at two different prey densities. I demonstrate that results obtained from the two designs differed when two species of intertidal crab foraged together on shared mussel prey. I show that differences in the relative strength of interference between conspecific and heterospecific predators lead to qualitatively opposite results using the additive and substitutive experimental designs,

and that the difference in results obtained using the two designs increased with prey density.

Natural History

To examine the impacts of multiple predators on shared prey, I used two established invasive predators on the East Coast of North America, the European green crab *Carcinus maenas*, and the Asian shore crab *Hemigrapsus sanguineus*. Both predators are common on the New England coast and presently are the dominant shore crabs in the southern Gulf of Maine. The two crab species are often found together (McDermott 1998) and may compete for food resources (Tyrrell and Harris 1999, Jensen et al. 2002). The blue mussel, *Mytilus edulis*, an important prey resource for both of these species (Tyrrell and Harris 1999, Lohrer and Whitlatch 2002), was used as shared prey in this experiment. Previous experiments with these two species foraging on shared amphipod prey demonstrated that both species decrease foraging effort in the presence of the other species (see Chapter 2). Thus I expected that their predation on mussel prey may not be additive. Additionally, both species decrease foraging effort in the presence of conspecifics (see Chapter 1).

The experiment was conducted on a semi-exposed beach at South Odiorne Point, New Hampshire, USA, that is dominated by various sized boulders and cobble overlying a substrate of sand and shell. Both species of crab are patchily abundant at this site (*C. maenas* density: 7.28 ± 7.71 m^{-2} [mean ± 1 std. dev.] and *H. sanguineus* density: 3.6 ± 5.97 m^{-2}; range = 0-48 and 0-38 individuals m^{-2} for each species, respectively). Additionally, individuals of the two species are found in close association, frequently

inhabiting space under the same rock. Mussels at Odiorne Point are mainly found attached sporadically underneath or around boulders and cobble. Mussel densities in lower intertidal regions of Odiorne Point where this experiment was conducted are highly variable: 198 ± 107 m^{-2} (Tyrrell and Harris 1999).

Methods

Experimental Design

I examined predation by *C. maenas* and *H. sanguineus* on mussels in field enclosures (0.6 × 0.5 × 0.3 m, $l \times w \times h$) that were constructed of lobster wire and lined by 0.5-cm plastic mesh, and were deployed at approximately mean low water. Small boulders were cleared from the substrate to allow for enclosure placement and were subsequently placed inside enclosures to mimic ambient habitat. Naturally occurring flora and fauna were not removed from these boulders and could have been used as an alternative prey source by either predator. Other potential prey items within experimental enclosures included urchins, limpets, snails, amphipods, polychaetes, small sea stars (< 2 cm diam.), brittle stars, small fish, juvenile crabs, and macroalgae. Evidence of predation was at times apparent on some of these alternative prey. While this may dilute effects of predation on the focal prey (mussels), it was desirous to further approximate the natural habitat where the predators have multiple prey choices.

I used the full complement of predator treatments necessary to compare the additive and substitutive experimental designs: one *C. maenas*, two *C. maenas*, one *H. sanguineus*, two *H. sanguineus*, one *C. maenas* + one *H. sanguineus*, and a no predator control. Adult males of both species were used, as female *H. sanguineus* in preliminary

experiments did not consume the size of mussels used in this experiment (10-20 mm shell length). Adult *C. maenas* in the Gulf of Maine are typically much larger than adult *H. sanguineus*, and this was reflected in the carapace widths of crabs used in these experiments (*C. maenas*: 53 ± 7 mm [mean ± S.D.]; *H. sanguineus*: 24 ± 3 mm).

To provide multiple opportunities for comparison between the additive and substitutive designs, I conducted experiments at two mussel densities that were both within the middle range of mussel densities at Odiorne Point. Henceforth, I refer to these as high (80 mussels per enclosure, = 267 m^{-2}) and low (40 mussels per enclosure, = 133 m^{-2}) densities. Each of the six predator treatments listed above were conducted at each of these prey densities, thus allowing for two separate comparisons between the additive and substitutive designs.

Mussels were introduced into experiments by haphazardly scattering them within enclosures and allowing them to form byssal thread attachments between or under boulders. Crabs were introduced to the enclosures 24 h later. Crabs were allowed to forage for six days, following which, the contents of each enclosure was removed and the number of surviving mussels was counted. Each treatment was replicated five times, once during each of five separate, consecutive trials conducted during July and August 2004. Individual animals were only used in a single trial.

Data Analysis

I determined whether an emergent multiple predator effect occurred by comparing observed prey survival when both predator species foraged together to expected values in the absence of risk reduction or risk enhancement. Expected survival assuming the

predators have independent effects ($E_{1,2}$) can be calculated for the additive experimental design using the number of prey surviving when single predators of each species foraged alone as follows (Billick and Case 1994, Vonesh and Osenberg 2003, Vance-Chalcraft and Soluk 2005a):

$$E_{1,2} = (N_1 \times N_2)/N_c \qquad (3.1)$$

where N_1, N_2, and N_c are the number of prey that survive each trial with *C. maenas*, *H. sanguineus*, and the no predator control, respectively. When prey survival is 100% in the no-predator control, equation 1 yields the same expected consumption as the multiplicative risk model proposed by Soluk (1993) and commonly employed by researchers using an additive experimental design with prey depletion (Sih et al. 1998). Because equation 1 explicitly includes survival in the absence of predators, it may be preferred in the presence of predator-free "background" prey mortality. Data can be statistically compared to this expected null model by conducting a two-way ANOVA on log transformed prey survivorship data, with the presence/absence of each predator species treated as a separate factor (Billick and Case 1994, Sih et al. 1998). A significant interaction term between the two factors indicates the presence of an emergent effect of combining the two predator species. Because I examined the additivity of *C. maenas* and *H. sanguineus* at two prey densities, I conducted a three-way ANOVA ($\alpha = 0.05$), analogous to the two-way ANOVA just described, but with high and low prey density as two levels of a third factor. A significant two-way interaction (*C. maenas* × *H. sanguineus*) would thus still indicate the presence of nonadditivity, and a significant three way interaction (*C. maenas* × *H. sanguineus* × prey density) would indicate that emergent effects of the two predators change with prey density.

I next assessed the effects of combining both predator species together while holding total predator density constant using the substitutive experimental design. I again compared observed prey survival to expected survival if each predator species has independent effects. I used a null model of expected survival derived from the same independent effects model from which Equation 3.1 was derived (Billick and Case 1994). The original model (equations 11-14 in Billick and Case [1994]) was modified for use with the substitutive design by dividing prey mortality rates when predators were combined by two because the substitutive design uses half the number of predators in the combined predator treatment as in the single predator treatments. This yielded:

$$E_{1,2} = (N_{1,1} \times N_{2,2})^{0.5} \qquad (3.2)$$

where $N_{1,1}$ and $N_{2,2}$ are the number of prey surviving when foraged on by pairs of *C. maenas* and *H. sanguineus*, respectively. Expected prey survival ($E_{1,2}$) was calculated separately for each replicate trial. The presence of an emergent multiple predator effect was then detected using ANOVA with the number of prey surviving to the end of each trial as the response variable, observed and expected as two levels of one factor, and high and low prey density as two levels of a second factor (Vance-Chalcraft et al. 2004, Vance-Chalcraft and Soluk 2005b). This was followed by planned linear contrasts to separately compare observed and expected prey survival at high and low prey densities. Previous studies have used the average of the single species treatments as the null model when using a substitutive experimental design (e.g., Siddon and Witman 2004). For comparison I also analyzed the data using this null model. However, as this did not alter the patterns seen or the conclusions drawn from the study, only results using equation 2 are given here.

I conducted an additional statistical test to more fully understand the influence of predator density on predation by *C. maenas* and *H. sanguineus* when the two species foraged alone. I conducted a two-way ANOVA ($\alpha = 0.05$) on log transformed prey mortality (to correct for heteroscedasticity in the data) with predator identity (*C. maenas* or *H. sanguineus*) as one factor, and predator density (one or two individuals) as a second factor.

Trial was initially included as a blocking factor in each of these analyses described above, but was later removed as it was not responsible for a significant amount of the variation in any of the analyses. Removal of the blocking factor did not alter the conclusions of the analyses. Statistical analyses were performed using JMP IN (SAS Institute Inc. 2003) version 5.1.

Results

No predator mortality occurred during any of the trials. Approximately 50% of the mussel prey were consumed by *C. maenas* (significant main effect of *C. maenas*, $p < 0.0002$ Table 1A, Fig. 3.1). While 25-30% of the prey were consumed by *H. sanguineus*, the decrease in prey survival was not statistically significant (main effect of *H. sanguineus*, $p = 0.95$, Table 1A, Fig. 3.1). Single predators of both species more than doubled their prey consumption with increasing prey density (significant main effect of prey density, $p = 0.0001$; and there was no significant interactions between prey density and either species, $p = 0.59$ for *C. maenas* and $p = 0.85$ for *H. sanguineus*; Table 3.1A, Fig. 3.1). Similarly, when two conspecifics foraged together, increasing prey density

caused *C. maenas* and *H. sanguineus* to increase predation by 50% and 200%, respectively (significant effect of prey density, $p < 0.0001$, Table 3.1B, Fig. 3.1).

Prey survival when the two predator species foraged together was greater than expected based on the additive experimental design at both prey densities examined (significant *C. maenas* × *H. sanguineus* interaction, $p = 0.04$; and nonsignificant three-way interaction, $p = 0.62$; Table 3.1A, Fig. 3.1, 3.2). However, qualitatively opposite results were obtained using the substitutive experimental design, and results depended on prey density. Prey survival when the two predator species foraged together at the high prey density was less than expected based on the substitutive experimental design (significant difference between observed and expected in linear contrast, $p = 0.05$; Table 3.1B, Fig 3.1, 3.2), and was similar to expected at low prey density (nonsignificant difference between observed and expected in linear contrast, $p = 0.47$; Table 3.1B, Fig 3.1, 3.2).

Finally, each predator species consumed the same number of mussels in single-species treatments regardless of whether one or two predators were present (nonsignificant main effect of predator density, $p = 0.69$; and nonsignificant interaction of predator density × predator species, $p = 0.19$; Table 3.1C, Fig. 3.1).

Discussion

Results of this study are consistent with previous studies that have examined predation by these and other crab species. I found that *C. maenas* consumed approximately 50% more mussels than did *H. sanguineus* (Fig. 3.1). Previous studies with smaller mussels (< 10 mm shell length) have reported higher predation rates for both

crab species than those reported here (Brousseau et al. 2001, Lohrer and Whitlatch 2002) and reported approximately 30% higher consumption rates for adult *C. maenas* than for adult *H. sanguineus* (Lohrer and Whitlatch 2002). The lower consumption rates and greater disparity between the consumption rates of the two crabs observed here may result first from the use of larger mussel prey than in previous studies, as *H. sanguineus* preferentially consumes mussels smaller than 10 mm shell length (Bourdeau and O'Connor 2003), and second from the inclusion of alternative prey items in the experimental enclosures, as *H. sanguineus* is more omnivorous than *C. maenas* (Tyrrell and Harris 1999). Finally, the findings here that predation increases with prey density and decreases with predator density are consistent with previous studies of crab predation on bivalve prey (Mansour and Lipcius 1991, Clark et al. 1999, Taylor and Eggleston 2000, Sietz et al. 2001, Mistri 2003).

Results of this study indicate that the strength of multiple predator effects (both risk reduction and risk enhancement) can vary with prey density. Previous studies using additive experiments have also reported increases in both risk reduction (Soluk 1993) and risk enhancement (Losey and Denno 1998) with increasing prey density, while others have reported similar levels of risk reduction across prey densities (Vance-Chalcraft and Soluk 2005b). Limited behavioral options for mussel prey imply that nonadditive effects in this study were likely due to changes in predator foraging in the presence of competitors. Increased departure from expected results at high prey densities may be attributed to the increased foraging effort of predators in all treatments at high prey densities (Fig. 3.1). Higher foraging effort may, in turn, result in more frequent interactions between crabs, thus increasing the magnitude of the effects of interference.

While these results were consistent with established foraging ecology of crab predators and previous studies demonstrating the impacts of prey density on multiple predator effects, they highlight a discrepancy between conclusions that may be drawn from additive and substitutive experimental designs, and demonstrate that the two cannot be used interchangeably. Emergent effect of the two predators in my experiment depended on prey density and which experimental design was used (Fig. 3.2). Prey survival was greater than expected based on the additive experimental design at both prey densities. However, using the substitutive experimental design, prey survival was not different than expected at low prey density, and was lower than expected at high prey density. Taken independently these results would be interpreted as risk reduction at both prey densities using the additive design, with no emergent effect at low prey density and risk enhancement at high prey density using the substitutive design.

The discrepancy between the results of the two approaches can be attributed to how the two experimental methods "deal with" intraspecific interference and its strength relative to interspecific interference. The detection of risk enhancement with the substitutive design does not imply that predator facilitation occurred. Rather, interference occurred between the two species, decreasing predation rates below those observed when individuals of each species foraged independently (Fig. 3.1). Using additive experiments, many researchers with similar results have concluded that risk reduction occurs in their study systems (see Chapter 2 and Sih et al. 1998, Finke and Denno 2002, Crumrine and Crowley 2003, Harvey et al. 2004, Warfe and Barmuta 2004). However, per capita predation by both species was higher when single individuals foraged than when two conspecifics foraged together, indicating that intraspecific

interference also decreased predation rates (Fig. 3.1). Further, intraspecific interference in my experiment was stronger than interspecific interference (i.e., per capita predation decreased more when conspecifics were combined than when heterospecifics were combined; Fig. 3.1). This is consistent with a laboratory behavioral study in which conspecific pairs of these predators foraging on mussels spent 68% more time in aggressive behaviors than heterospecific predator pairs (author, unpubl. data). The substitutive design, in effect, compares the impacts of interspecific interference relative to intraspecific interference. Therefore, while the two predator species did not facilitate one another's prey consumption, risk of predation was higher for prey when heterospecific predators foraged together than when conspecific predators foraged together (i.e., risk enhancement).

Four previously published studies employed the same treatments used here to examine systems with multiple predators (Evans 1991, Peckarsky 1991, Vance-Chalcraft et al. 2004, Vance-Chalcraft and Soluk 2005a). Of these, two examined prey mortality/survival, and therefore lend themselves to comparison of the additive and substitutive experimental design for detecting emergent effects of multiple predators (Vance-Chalcraft et al. 2004, Vance-Chalcraft and Soluk 2005a). I obtained survivorship data from the original authors of these studies and then used equations 1 and 2 to determine expected prey survival when predator species foraged together (Table 3.2). Only average survival across all replicates of a given treatment was available, and therefore no estimate of error is presented. Consistent with this study, a discrepancy exists in the direction of emergent effects in six of the seven multiple predator comparisons, with the additive design detecting risk reduction, and the substitutive design

detecting risk enhancement (Table 3.2). A single comparison detected risk reduction with both designs, but the magnitude of risk reduction based on the additive design was nearly an order of magnitude greater than that based on the substitutive design.

The inconsistencies between results obtained with the additive and substitutive designs in this and the previous studies indicates a consistent trend that interference with conspecific predators often reduces predation as much as, or more than, interference between heterospecific predators. This finding highlights the importance of including intraspecific interactions when assessing the impacts of multiple predator species to ensure that observed multiple predator effects are an emergent result of interactions between predator species, and not simply an outcome of altering predator density (Sih et al. 1998).

It should also be noted that mechanisms besides predator interference could also lead to conflicting results from the two experimental methods. For example, changes in prey behavior are at times the underlying mechanism that causes risk reduction (Eklöv 2000) or risk enhancement (Swisher et al. 1998). Prey often alter behavior proportionally to the threat of predation (Lima 1998), which can in turn be influenced by predator density. If prey alter behavior in response to total predator density, then additive experiments that confound changes in total predator density and predator species richness may lead to erroneous conclusions. Similarly, if prey respond to each predator species individually (rather than to total predator density) (e.g., DeWitt and Langerhans 2003), then substitutive experiments that confound changes in individual predator species density and predator species richness could lead to erroneous conclusions.

Thus in this study system, as well as others where predator density is an important component of interactions between predators and prey, the most complete understanding of the effects of multiple predators may be obtained using an experimental design that combines additive and substitutive components, as has previously been encouraged (Sih et al. 1998). Using only the additive design would have led to the conclusion that the two species interfere, but the roles of total predator density and unique interspecific effects would have been unclear. Predation that is greater than expected was detected with the substitutive design; thus using only this design would have led to the false conclusion that these two predators facilitate each other's predation. Only by using both methods together is it possible to obtain the full picture that these species interfere with each other, but that this interference does not decrease per capita predation rates to the same extent as conspecific interference.

The need to develop predictive patterns in the effects of multiple predators on shared prey highlights perhaps the greatest shortcoming of using the different experimental designs interchangeably in examining predation by multiple species. When different experimental designs are used, interference between predator species in one study, for example, is not equivalent (or comparable) to that in another. Therefore, it becomes more difficult to detect patterns across studies in the strengths of emergent multiple predator effects that can eventually facilitate predictions. Thus, using a combined additive and substitutive experimental design not only provides more information on the system under study, but should also advance our understanding of the effects of multiple predators across systems at an accelerated pace.

Table 3.1 Results of ANOVAs used to compare observed predation by *C. maenas* and *H. sanguineus* to expected predation based on an additive (part A) and a substitutive (part B) experimental design, and to examine the influence of predator density on prey consumption (part C). Degrees of freedom in linear contrasts portion of part B are given as Numerator, Denominator.

A. Test of additive design (three-way ANOVA)

Source	*df*	*SS*	*F*	*p*
C. maenas	1	2.7936	17.521	0.0002
H. sanguineus	1	0.0008	0.005	0.946
Prey density	1	3.0858	19.354	0.0001
C. maenas × *H. sanguineus*	1	0.7086	4.445	0.043
C. maenas × Prey density	1	0.0463	0.291	0.594
H. sanguineus × Prey density	1	0.0058	0.036	0.850
C. maenas × *H. sanguineus* × Prey density	1	0.0412	0.259	0.615
Error	32	5.1022		

B. Test of substitutive design (two-way ANOVA)

Source	*df*	*SS*	*F*	*p*
Observed/Expected	1	150.4717	2.584	0.322
Prey density	1	3242.1151	55.669	<0.0001
Observed/Expected × Prey density	1	235.5829	4.045	0.062
Error	16	931.8226		
Linear Contrast				
Obs vs. Exp at high prey density	1,16	381.3051	6.547	0.021
Obs vs. Exp at low prey density	1,16	4.7494	0.082	0.779

C. Effect of predator density (two-way ANOVA)

Source	*df*	*SS*	*F*	*p*
Predator species	1	18.9498	24.826	<0.0001
Predator density	1	0.1234	0.162	0.690
Predator species × predator density	1	1.3340	1.748	0.195
Error	36	27.4793		

Table 3.2 Comparison of additive and substitutive experimental designs from previously published studies. Predicted survival was calculated (using equations 3.1 and 3.2) from average survivorship across all replicates. Observed survival that is greater than or less than expected indicates risk reduction or risk enhancement, respectively. Mayflies were used as prey in each of these studies

Predators	**Predicted**		**Observed**	**Publication**
	Additive	**Substitutive**		
Dragonfly and hellgrammite	0.325	0.571	0.600	Vance-Chalcraft et al. 2004
Dragonfly and hellgrammite	0.582	0.694	0.674	Vance-Chalcraft and Soluk 2005b
Dragonfly and darter	0.465	0.666	0.604	Vance-Chalcraft and Soluk 2005b
Dragonfly and creek chub	0.555	0.710	0.659	Vance-Chalcraft and Soluk 2005b
Hellgrammite and darter	0.428	0.618	0.537	Vance-Chalcraft and Soluk 2005b
Hellgrammite and creek chub	0.511	0.659	0.637	Vance-Chalcraft and Soluk 2005b
Creek chub and darter	0.409	0.632	0.478	Vance-Chalcraft and Soluk 2005b

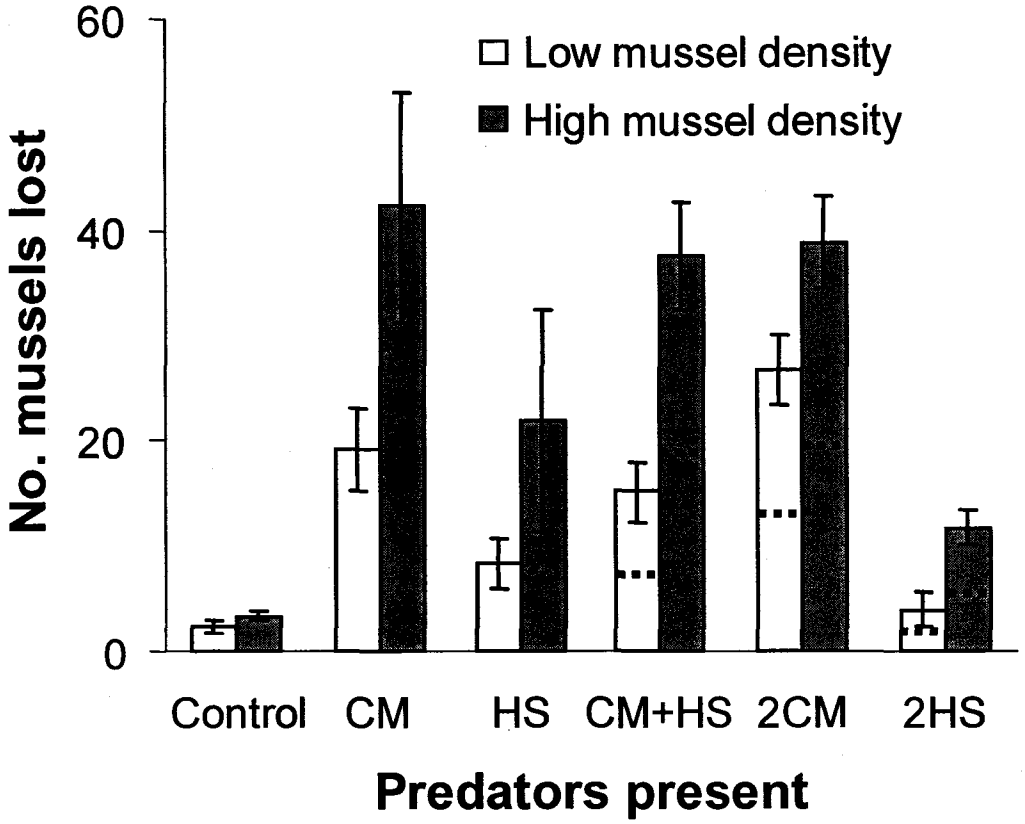

Figure 3.1 Number of mussel prey lost (mean ± 1 SE, n = 5) at low (133 m^{-2}) and high (267 m^{-2}) mussel densities by *C. maenas* and *H. sanguineus* foraging as single individuals and in heterospecific and conspecific pairs. Abbreviations on x-axis are as follows: *C. maenas* (CM) and *H. sanguineus* (HS). The average per capita number of mussels consumed at low and high mussel densities is also shown as dotted lines for treatments with two crabs foraging together. No predators were present in the control

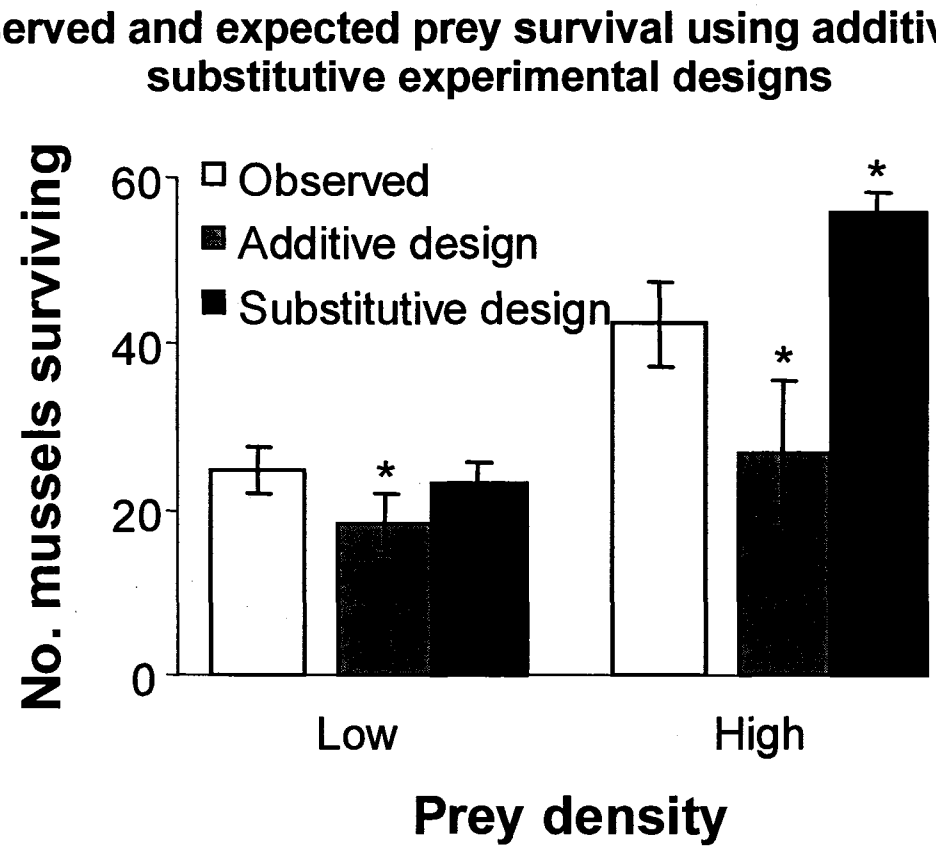

Figure 3.2 Observed and expected mussel prey survival based on the additive and substitutive experimental designs at low and high mussel densities. Expected values based on the additive and substitutive experimental designs were determined using equations 1 and 2, respectively. An asterisk (*) indicates expected survival that was different than observed for ($p \leq 0.05$). Bars are mean ± 1 SE ($n = 5$)

CHAPTER 4

INFLUENCE OF PREDATOR DENSITY ON NONINDEPENDENT EFFECTS OF MULTIPLE PREDATOR SPECIES

Abstract

Interactions between multiple predator species are frequent in natural communities and can have important implications for shared prey survival. Predator density may be an important component of interactions between predator species, as the frequency of interactions between species are largely determined by species density. Here we experimentally examine the importance of predator density for interactions between predator species and subsequent impacts on prey. We show that aggressive interactions among the predatory shore crabs *Carcinus maenas* and *Hemigrapsus sanguineus* increase with predator density, yet did not increase as fast as negative interactions between conspecifics. At low density, interactions between conspecific and heterospecific predators had similar inhibitory impacts on predator function, whereas conspecific interference was greater than interference from heterospecifics at high predator density. Thus the impact of conspecific interference at high predator density was sufficient that interactions with a second predator species had no additional impact on per capita predation. Spatial and temporal variability in predator density is a ubiquitous characteristic of natural systems that should be considered in studies of multiple predator species.

Introduction

Density is an important factor contributing to the overall function and impact of species within ecological communities. Density is particularly important in interactions between species, and its consideration has been instrumental in understanding fundamental ecological processes that occur between interacting species, including interspecific competition (Connell 1961), consumer-resource interactions (Volterra 1926), predator functional responses (Holling 1959), and resulting trophic cascades (Hairston et al. 1960).

One type of species interaction that has recently received much attention is the combined effects of multiple predator species (Sih et al. 1998). Predator species that share the same prey frequently interact, altering the influence of one or both species on prey so that their impacts are nonindependent. When predator nonindependence occurs, prey mortality as predator species forage together is either less than expected based on prey mortality when each predator species forages separately (risk reduction) or greater than expected (risk enhancement). Experimental examinations of nonindependent effects of multiple predator species have focused mainly on behavior (i.e., trait-mediated interactions), such as conflicting responses of prey to different predator species (Soluk 1993, Losey and Denno 1998, Swisher et al. 1998, Eklöv and VanKooten 2001, Crumrine and Crowley 2003, DeWitt and Langerhans 2003, Harvey et al. 2004), or aggression between predators and predator induced changes in foraging behavior (see Chapters 1, 2, and 3 and Peckarsky 1991, Soluk 1993, Eklöv and Werner 2000, White and Eigenbrode 2000, Crumrine and Crowley 2003, Lang 2003, Warfe and Barmuta 2004).

These studies have amply demonstrated the importance of individual behavioral traits in systems with multiple predator species; however, species density is also important. This fact has been empirically shown for prey, as the strength of nonindependent effects of multiple predator species (i.e., the strength of risk reduction or risk enhancement) can vary with prey density (see Chapter 3 and Soluk 1993, Losey and Denno 1998, Vance-Chalcraft and Soluk 2005b). The importance of predator density has only received cursory attention, dealing mainly with changes in the way that additive and substitutive experimental designs manipulate the relative densities of two interacting predator species (see Chapter 3). However, an extensive search of the literature revealed no studies that systematically varied predator density in multiple predator combinations in an effort to examine the influence of predator density in eliciting nonindependent effects of multiple predators.

In contrast to studies of multiple predator species, the importance of predator density when only a single predator species occurs is well-documented. Interference among conspecific predators generally increases with predator density due to higher frequency and intensity of interactions (Mansour and Lipcius 1991, Clark et al. 1999, Mistri 2003, Schenk et al. 2005, Smallegange et al. 2006), resulting in lower per capita effects of predators on prey (Arditi and Ginzburg 1989, Arditi and Akcakaya 1990, Clark et al. 1999, Abrams and Ginzburg 2000, Mistri 2003). Similarly, the behaviors that elicit nonindependent effects of multiple predator species may interact with predator density, potentially resulting in density-dependent strengths of risk reduction or risk enhancement. Thus the overall implications for prey of interacting predator species may depend on spatially variable predator densities and the resulting influence on predator interactions.

Here we investigate the combined impacts of two co-occurring predators across a range of densities in an effort to determine how predator density affects the way that consumption by multiple predator species combines. *Carcinus maenas* and *Hemigrapsus sanguineus* are two predatory crabs that are invasive to the Atlantic coast of the United States and are presently the dominant shore crab species along much of the coast. These species utilize similar habitats and prey resources (Tyrrell and Harris 1999, Lohrer et al. 2000), resulting in interference competition between the two (Jensen et al. 2002). Aggressive interference among crab predators frequently reduces prey consumption (Mansour and Lipcius 1991, Clark et al. 1999, Taylor and Eggleston 2000, Sietz et al. 2001, Mistri 2003, Smallegange et al. 2006), and previous work with these particular species demonstrates that risk reduction occurs as a result of predator interference when these two species forage together (see Chapters 1, 2, and 3).

On the regional scale, the densities and distributions of these two species have shifted dramatically over the last decade as the introduction of *H. sanguineus* appears to have decreased the numbers of *C. maenas* in rocky intertidal habitats along its northward range expansion, which has presently reached central Maine (Lohrer and Whitlatch 2002a). As a result, the region of overlap between these species has steadily shifted northward. Currently this region of overlap occurs in the central Gulf of Maine, from Massachusetts to mid-coast Maine. Both species are found abundantly at our field site at Odiorne Point, NH, the midpoint of this region (see Chapter 2). This site is delineated into a series of coves, each separated by ≈50-100m, and aggregation of predators to coves with abundant food and refuge habitat results in a positive correlation in the densities of *C. maenas* and *H. sanguineus* across coves (see Chapter 5). This system thus provides an

excellent opportunity to examine the (in)dependence of predation by two predator species whose densities naturally covary across a wide range.

Using field and laboratory experiments, we examined how predator density influences the combined effects of *C. maenas* and *H. sanguineus* on the blue mussel *Mytilus edulis*, an important food source for both species (see Chapter 5 and Ebling et al. 1964, Elner 1981, Lohrer and Whitlatch 2002b, Bourdeau and O'Connor 2003, DeGraaf and Tyrrell 2004). We also compare the influence of predator density on heterospecific predator interactions to the effect of density on interactions between conspecific predators. Finally, we observe predator behavior to determine whether the effects of predator density can be explained mechanistically by changes in aggressive interactions between predators.

Methods

Field Experiment on Impacts of Predator Density

Field experiments were conducted on a semi-exposed beach at South Odiorne Point, New Hampshire. This site is characterized by a series of coves separated by bedrock outcroppings. The dominant substrate is boulders overlying a substrate of sand and shell. Low tide sampling found densities of large *C. maenas* (>30 mm CW) ranging from 0-28 m^{-2}, while densities of large *H. sanguineus* (>20 mm CW) ranged from 0-16 m^{-2} between coves (see Chapter 5). We conducted experiments in a cove with relatively low densities of both crabs (*C. maenas*: 2.8 ± 2.8 m^{-2}, *H. sanguineus*: 1.5 ± 1.8 m^{-2}, mean ± SD) in order to minimize the influence of ambient crabs.

Experiments were conducted in enclosures (0.6×0.5×0.3 m) deployed at approximately 0.5 m above mean low water. Enclosures were constructed of lobster wire and were lined with 0.5 cm plastic mesh. Small boulders that had been cleared from the substrate to allow for placement of experimental enclosures were placed inside enclosures to mimic ambient habitat. Naturally occurring flora and fauna were left on boulders, so that a naturally occurring array of prey species was available inside enclosures. These included urchins, limpets, snails, amphipods, polychaetes, small sea stars (<2 cm diameter), brittle stars, small fish, juvenile crabs, and macroalgae. Thus, although we focused our experiments on consumption of mussel prey, predators were not artificially limited in their food choices. While this may have diluted impacts on focal prey, this was desirable in order to provide a more realistic picture of predation in the natural habitat where these omnivorous predators have a variety of prey to choose from.

After removal of naturally occurring mussels, fifty experimental mussels that had been collected from the surrounding area were scattered haphazardly into enclosures 24 h before inclusion of predators to allow time for byssal thread attachment. This mussel density (167 m^{-2}) is similar to natural densities of mussels in the lower intertidal regions of Odiorne Point (198±197 m^{-2}) where the experiment was conducted (Tyrrell and Harris 1999). We used mussels in the size range of 15-20 mm shell length, the preferred size of mussel prey for adult *C. maenas* (Elner and Hughes 1978). Using this size mussel likely decreased mussel consumption rates by *H. sanguineus*, as this size mussel is slightly larger than their preferred size (Bourdeau and O'Connor 2003). However, while not the preferred size, *H. sanguineus* can and does consume this size mussel prey (McDermott 1998, DeGraaf and Tyrrell 2004, Griffen pers. obs.).

To examine the impact of predator density on multiple predator effects, we experimentally increased the density of *C. maenas* and *H. sanguineus* simultaneously (rather than orthogonally), mimicking the positive correlation between the two species observed between coves at our field site (see Chapter 5). We used an experimental design that combined components of the additive and substitutive experimental designs commonly in use (see review in Chapter 3). This allowed us to examine the influence of predator density on interspecific interference and its importance relative to intraspecific interference.

Experimental treatments included each species foraging alone at densities of 1, 2, 3, 4, 6, and 8 individuals per enclosure (equivalent to approximately 0-26 crabs m^{-2}), and both species foraging together at densities of 1, 2, 3, and 4 individuals of each species per enclosure. This range of densities is similar to the range observed at our field site for large *C. maenas*, is greater than that observed at our field site for large *H. sanguineus*, but is well within the range of densities observed for *H. sanguineus* at sites in its invaded range (Brousseau et al. 2003). Each of these 16 treatments and the no predator control were replicated five times, once during each of five blocked trials during June and July 2004. Adult males (*C. maenas* 49.5 ± 7.2 and *H. sanguineus* 23.9 ± 2.5 mm CW) that had been starved for 24 h to standardize hunger were allowed to forage in each trial for six days, following which we removed the content of each enclosure and assessed the number of surviving mussel prey. No other predators that potentially consume mussels were included in experimental cages (e.g., no whelks or large sea stars), thus prey mortality was attributable to crab predation.

To examine the difference in predation by the two crabs in our experiment and the influence of predator density on each species individually, we compared per capita predation rates of the two species in single-species treatments using an ANCOVA on log transformed per capita predation rates, with species as a fixed factor and predator density as a covariate.

The experimental treatments listed above allowed us to compare observed prey survival when one, two, three, and four predators of each species foraged together to expected survival. At each of these predator densities, we calculated two different values for expected prey survival. We calculated expected prey survival when predators are combined ($E_{1,2}$) in an additive fashion (based on multiplicative risk of predators): $E_{1,2}=N_1\times N_2/N_c$, where N_1, N_2, and N_c are the number of prey that survive each trial with *C. maenas*, *H. sanguineus*, and the no predator control (see Chapter 3 and Billick and Case 1994, Vonesh and Osenberg 2003, Vance-Chalcraft and Soluk 2005a). Prey survival that is different from expected based on this model would indicate that interactions between the two predator species alter their combined predation on shared prey.

We also calculated prey survival when predators are combined in a substitutive fashion: $E_{1,2}=(N_{1,1}\times N_{2,2})^{0.5}$, where $N_{1,1}$ and $N_{2,2}$ are the numbers of prey surviving when foraged on by conspecific combinations of *C. maenas* and *H. sanguineus*, respectively (see Chapter 3). This model compares predator interference in treatments with multiple predator species to interference among predators of the same species at the same total density. Prey survival that is different from expected based on this substitutive model

would thus indicate that heterospecific predator interference has a different effect on prey consumption than conspecific predator interference (see Chapter 3).

We compared observed prey survival to both of these estimates of expected prey survival using separate two-way ANOVAs on prey survival with observed and expected as two levels of a fixed factor and predator density as a fixed factor (four levels). This was followed by planned linear contrasts of observed and expected survival at each predator density.

Laboratory Examination of Predator Aggression at Different Densities

We examined aggression by *C. maenas* and *H. sanguineus* in a laboratory experiment in which each species foraged alone or together at different predator densities. Experiments were conducted during July and August 2004 in 0.5 × 0.4 m polypropylene tanks with flowing seawater at the Shoals Marine Laboratory, Isles of Shoals, ME. To facilitate visual observations, refuge habitat inside the tanks was simple (compared to field refuge) and consisted of a single, 20-cm diameter rock placed in the center of each tank, overlying two centimeters of sediment. Fifty *M. edulis* (15-20 mm shell length) were scattered inside each experimental tank 12 h before the start of the experiment. We used single and multiple predator species combinations at three different predator densities, resulting in nine different predator treatments (single species treatments: 2, 4, or 8 *C. maenas* or *H. sanguineus*; multiple species treatments: 1 *C. maenas* + 1 *H. sanguineus*, 2 *C. maenas* + 2 *H. sanguineus*, or 4 *C. maenas* + 4 *H. sanguineus*).

Crabs, with identifying numbers painted on carapaces, were placed in tanks 2 h before data collection started (*C. maenas*: 46.5 ± 8.2 and *H. sanguineus*: 23.4 ± 2.8 mm CW). We collected data on all crabs within each treatment, yielding more observations in treatments with higher crab densities. Replication was thus unbalanced to equalize the total number of individuals of each species (12) at each density on which observations were made. Observations were made under red lights to minimize disturbance to crabs.

We recorded the behavior of each crab in a tank at six-minute intervals for two hours (yielding a total of 20 observations per crab). This type of instantaneous scan sampling requires that behaviors from one scan to the next be independent. We verified that a six-minute interval between observations was sufficiently long to ensure independence of behaviors by determining the proportion of six, twelve, or eighteen minute intervals over which the behavior of a given crab changed. We did this for each crab within the mixed species treatment with eight crabs (as this treatment provided the most data within a single treatment to make the comparison for both species). We used separate ANOVAs for each species to compare the proportion the six, twelve, or eighteen minute time intervals over which behavior changed.

We were particularly interested here in aggressive behaviors, which we defined as fighting, display of threat behavior (extending chelipeds), or displacement of one crab by another (see Smallegange et al. 2006 for a full explanation of identically defined aggressive behaviors). The proportion of the 20 observations in which any of these aggressive behaviors were displayed by individual crabs (arcsine square root transformed to achieve homogeneity of variance) was compared using three-way ANOVA, with

species (two levels), mixed species combinations (two levels: yes/no), and density (three levels) as fixed factors.

Results

Field Experiment on Impacts of Predator Density

C. maenas had much higher predation rates than *H. sanguineus* in single-species treatments of our field experiment (ANCOVA, $F_{1,56}$=93.86, P<0.0001, Fig. 4.1). Per capita predation rates of both species decreased with predator density (ANCOVA, $F_{1,56}$=44.87, P<0.0001, species×predator density effect $F_{1,56}$=0.07, P=0.79, Fig. 4.1). This was not simply an artifact of prey depletion, as only 39.2% ± 23.1% (mean ± SD) of mussels were consumed across all predator treatments and experimental trials. Predators also consumed non-focal prey species, as forensic evidence of this predation (e.g., crushed snail and urchin shells, etc.) were at times observed within experimental enclosures.

When *C. maenas* and *H. sanguineus* foraged together, the independence of their predator effects varied with predator density. Specifically, prey survival was greater than expected based on the additive model (i.e., risk reduction occurred) for the two lowest predator densities (ANOVA with planned linear contrasts; one predator of each species: $F_{1,32}$=4.21, P=0.05; two predators of each species: $F_{1,32}$=4.91, P=0.03; Fig. 4.2). In contrast, at the two highest predator densities, prey survival was not different from expected based on the additive model, indicating that at high densities the two species had independent effects (ANOVA with planned linear contrasts; three predators of each species: $F_{1,32}$=0.05, P=0.83; four predators of each species: $F_{1,32}$=0.08, P=0.78; Fig. 4.2).

Predator density also influenced the strength of conspecific predator interference relative to heterospecific interference. Conspecific and heterospecific interference were similar in strength at the two lowest predator densities, resulting in no difference between observed prey survival and expected based on the substitutive model (ANOVA with planned linear contrasts; one predator of each species: $F_{1,32}$=0.46, P=0.50; two predators of each species: $F_{1,32}$=1.10, P=0.30; Fig. 4.2). In contrast, at the two highest predator densities, observed prey survival was greater than expected based on the substitutive model, indicating that conspecific predator interference was stronger than heterospecific interference (ANOVA with planned linear contrasts; three predators of each species: $F_{1,32}$=4.66, P=0.04; four predators of each species: $F_{1,32}$=7.67, P=0.009; Fig. 4.2).

Laboratory Examination of Predator Aggression at Different Densities

Behaviors from one observation to the next changed approximately 48% of the time, and comparison with ANOVA indicated that this was not different between the six, twelve, or eighteen-minute time intervals for either crab species (*C. maenas* $F_{2,33}$=0.81, P=0.45, *H. sanguineus* $F_{2,33}$=60, P=0.56). Thus a six minute time interval between observations was sufficient to insure independent behaviors.

C. maenas displayed more aggressive behavior in our laboratory experiment than *H. sanguineus* ($F_{1,132}$=14.93, P=0.0002 Fig. 4.3). Aggression by both species increased with predator density ($F_{2,132}$=55.0, P<0.0001, species×density interaction $F_{2,132}$=1.07, P=0.35, Fig. 4.3). In general, predators were more aggressive when combined only with conspecifics than when combined with heterospecifics ($F_{1,132}$=12.93, P=0.0004, Fig. 4.3), though this trend was stronger for *C. maenas* than for *H. sanguineus* (mixed×species

interaction $F_{1,132}$=3.52, P=0.06). This was also influenced by predator density, as neither species showed more aggression when combined with conspecifics only than when combined with heterospecifics at the lowest predator density (*post hoc* linear contrasts, P>0.05, Fig. 4.3), while *C. maenas* was more aggressive when combined with conspecifics only than with heterospecifics at the highest predator density (*post hoc* linear contrast, P=0.005, Fig. 4.3).

Discussion

Nonindependent effects of multiple predator species do not occur uniformly wherever species overlap; rather, they are often spatially and temporally variable due to changes in various factors, including habitat complexity (Finke and Denno 2002, Warfe and Barmuta 2004), habitat type (see Chapter 2), and prey density (see Chapter 3 and Soluk 1993, Losey and Denno 1998, Vance-Chalcraft and Soluk 2005b). Our study demonstrates that effects of multiple predator species can also differ with predator density.

The relative predation rates of *C. maenas* and *H. sanguineus* in single-species treatments (Fig. 4.1) indicate that *C. maenas* was responsible for the majority of the prey consumption in treatments with both predator species. Thus, reductions in *C. maenas* mussel consumption as a result of interactions with *H. sanguineus* are likely responsible for the risk reduction observed at the two lowest predator densities (Fig. 4.2). This is consistent with previous studies where we have shown that *H. sanguineus* has strong negative impacts on mussel consumption by *C. maenas*, but that the reverse is not true (see Chapter 5).

At high predator densities conspecific predator interference had a greater impact on mussel survival than heterospecific interference (Fig. 4.2). This is also consistent with high levels of aggressive activity among *C. maenas* at high densities observed in our laboratory experiment. Thus, in our study system, *C. maenas* appears to be a stronger predator of mussel prey (Fig. 4.1) than *H. sanguineus.* Yet at low predator densities, interference from conspecifics and heterospecifics have similar negative impacts on *C. maenas* mussel consumption (Fig. 4.2 and 4.3). While at high predator densities, interference among *C. maenas* is so intense (Fig. 4.3) that adding another predator species has no significant additional impact on *C. maenas* foraging (Fig. 4.2).

Stronger aggression/interference between conspecifics than heterospecifics that we observed in both our field and laboratory experiments (Fig. 4.2 and 4.3) may be a common phenomenon. Theory states that competition among conspecific must be stronger than among heterospecifics in order for two species to coexist (Ricklefs 1993). Predator interference (competition for prey) may therefore frequently be strongest among conspecifics in systems with multiple predator species. Additionally, just as we found here, stronger effects of conspecifics may only become apparent at high predator densities, as this increases the overall importance of predator interference (Fig. 4.3).

Predator density may be particularly important in systems with intraguild predation (predation among predators). Intraguild predation can cause nonindependent effect of multiple predator species through prey switching by top predators (from consuming shared prey to consuming intermediate predators) and reduced foraging by intermediate predators in the presence of top predators (see Chapter 2 and Crumrine and Crowley 2003). These mechanisms may each become stronger with increased densities

of intermediate predators (Stephens and Krebs 1986) and top predators (Lima and Dill 1990, Lima 1998), respectively.

Finally, previous studies have highlighted the importance of prey density in determining the outcome of combined predation by multiple species (see Chapter 3 and Soluk 1993, Losey and Denno 1998, Vance-Chalcraft and Soluk 2005b). As with systems with a single predator species (Abrams and Ginzburg 2000), prey density and predator density may interact to influence the combined effects of multiple predator species. Because predators often aggregate to areas of high resource abundance (Fretwell and Lucas 1970), there is often a positive correlation between prey density and predator density. Thus the most broadly applicable examination of this interaction may be the case where predator and prey densities covary.

In conclusion, predator density is likely to have a large influence on multiple predator effects across most systems, just as it does in other ecological processes. Incorporating the range of natural predator densities into multiple predator studies should therefore improve the applicability of experimental results and increase our understanding of natural systems.

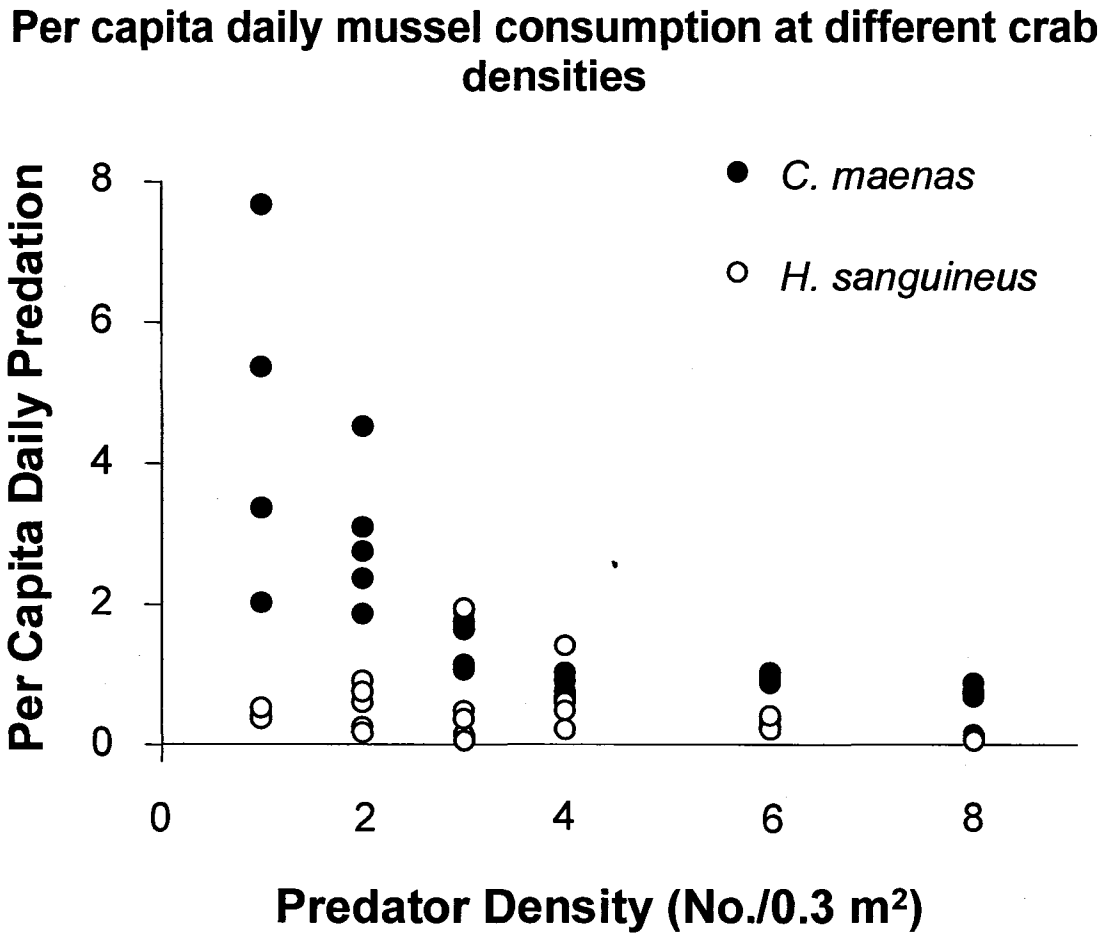

Figure 4.1 Daily per capita mussel consumption by *C. maenas* and *H. sanguineus* when present in single-species treatments at different densities in a field experiment. Dots represent mean prey consumption by all crabs within a single experimental enclosure.

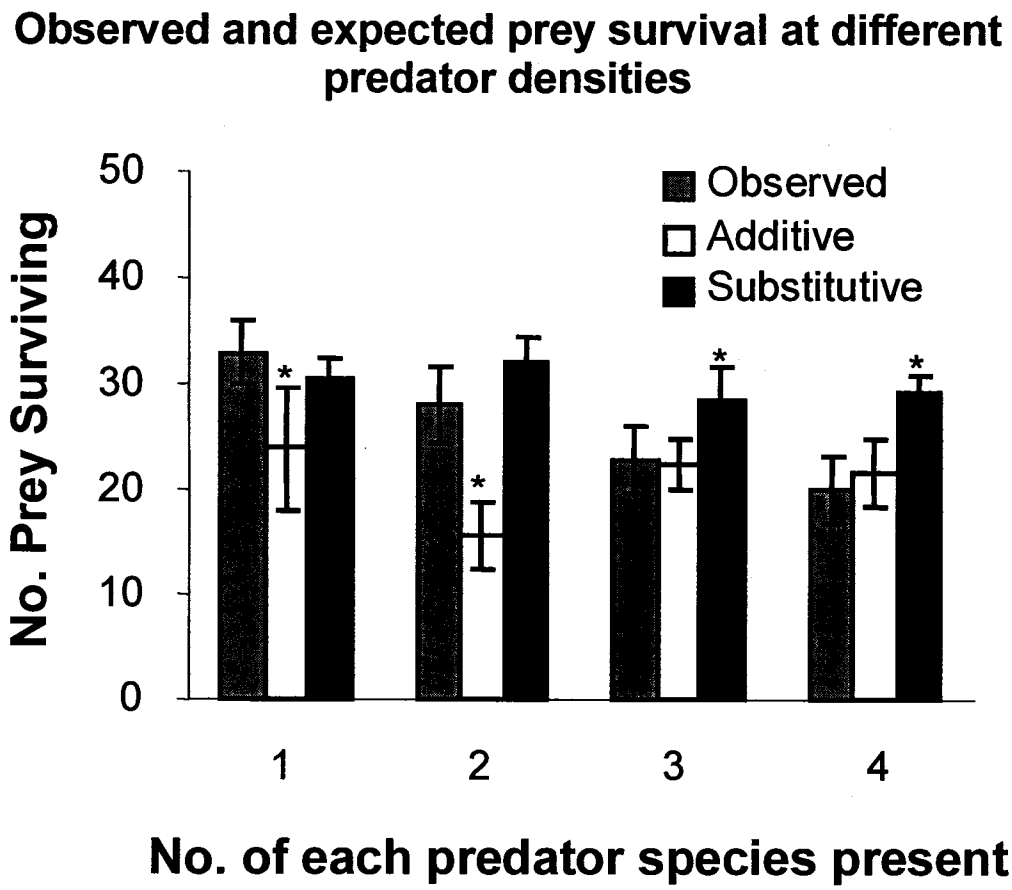

Figure 4.2 Comparison when predators are combined of observed prey survival to expected values if predators have independent effects. Expected survival was calculated using both an additive and a substitutive model. Bars are means ± SE (n = 5). Expected values that are significantly different from observed are indicated by asterisks, where * $p < 0.05$.

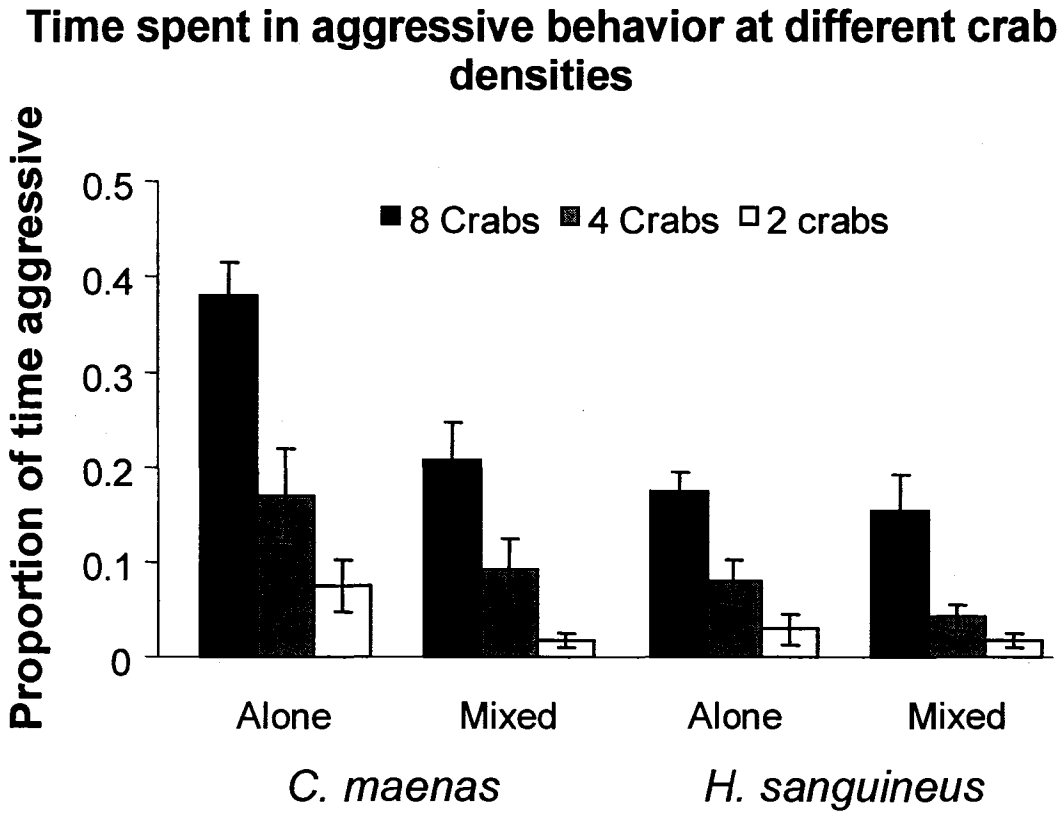

Figure 4.3 Proportion of time spent in aggressive interactions per crab by *C. maenas* and *H. sanguineus* (mean ± SE, n = 12) when paired with conspecifics only (alone) or in mixed species assemblages (mixed) (1:1 ratio of *C. maenas* and *H. sanguineus*) at different densities. Number of crabs shown is total number present.

CHAPTER 5

INHIBITION BETWEEN INVASIVES: A NEWLY INTRODUCED PREDATOR MODERATES THE IMPACTS OF A PREVIOUSLY ESTABLISHED INVASIVE PREDATOR

Abstract

With continued globalization, species are being transported and introduced into novel habitats at an accelerating rate. Interactions between invasive species may provide important mechanisms that moderate their impacts on native species. The European green crab *Carcinus maenas* is an aggressive predator that was introduced to the east coast of North America in the mid 1800s and is capable of rapid consumption of bivalve prey. A newer invasive predator, the Asian shore crab *Hemigrapsus sanguineus*, was first discovered on the Atlantic coast in the 1980s, and now inhabits many of the same regions as *C. maenas* within the Gulf of Maine. Using a series of field and laboratory investigations, we examined the consequences of interactions between these predators. Density patterns of these two species at different spatial scales are consistent with negative interactions because of similar resource use. As a result of these interactions, *C. maenas* alters its diet to consume fewer mussels, its preferred prey, in the presence of *H. sanguineus*. Decreased mussel consumption in turn leads to lower growth rates for *C. maenas*, with potential detrimental effects on *C. maenas* populations. Rather than an

invasional meltdown, this study demonstrates that, in the Gulf of Maine, this new invasive predator can moderate the impacts of the older invasive predator.

Introduction

Invasion of marine habitats by nonindigenous species is of increasing global concern (Ruiz et al. 1997) with significant ecological and evolutionary implications for native populations (Grosholz et al. 2000, Cox 2004). Interactions between native and invasive species are common, and influence not only native communities, but also the success and impact of invasive species (e.g., Herbold and Moyle 1986, Robinson and Wellborn 1988, Baltz and Moyle 1993, Reusch 1998, Crawley et al. 1999, Byers 2002, deRivera et al. 2005). Because of high rates of species introductions, many systems harbor multiple invasive species that also interact with each other, potentially moderating or exacerbating their impacts on native communities. Recent work has focused largely on synergism among invaders and the possibility of invasion meltdown (where previous invaders facilitate the success of subsequent invaders, Simberloff and Von Holle 1999, and see references in the review by Simberloff 2006). However, negative interactions may be just as important in determining the impacts of an invader.

In a review of interactions among invaders, Simberloff and Von Holle (1999) concluded that interactions with positive (+) effects on one species and negative (–) effects on the other are by far the most extensively documented. Mutualism (+/+), competition (–/–), and commensalisms (+/0) have been reported less frequently, and no instances of amensalism (–/0) have been reported. Thus, more studies are needed to assess the threat of invasional meltdown with multiple invasions (Simberloff 2006).

The types of interactions (both positive and negative) that occur between species depend in part on their ecological roles within the community (i.e., predator, herbivore, primary producer, etc.). Based on the competitive exclusion principle (Hardin 1960), negative interactions (either competition or amensalism) may be expected when species use similar resources or perform similar ecological roles (i.e., when they are functionally redundant, Lawton and Brown 1993, Rosenfeld 2002). In this study we demonstrate an amensal interaction in the trophic functions of two invasive predatory crabs, *Carcinus maenas* and *Hemigrapsus sanguineus*, by which resource use by the first invader is moderated through negative interactions with the subsequent invader.

C. maenas' many invasions have resulted in a cosmopolitan range that includes the east and west coasts of North America, South Africa, and Australia (Grosholz and Ruiz 1996). *C. maenas* was first noted on the Atlantic coast of North America in New York and New Jersey in 1817 (Say 1817), and spread into the Gulf of Maine by the early 1900s (Rathburn 1905). Because of its aggressive nature, *C. maenas* can have detrimental impacts on invaded communities (Grosholz and Ruiz 1996, Grosholz et al. 2000). Its frequent predation on molluscan prey (Ropes 1968) makes bivalve populations particularly vulnerable (e.g., soft-shelled clams, Glude 1955). The native blue mussel *Mytilus edulis*, an important species ecologically on open coast shores of New England (Menge 1976), is a major component of *C. maenas*' diet (Elner 1981). *C. maenas* can consume mussels at very high rates, with destructive consequences for mussel populations (Ebling et al. 1964).

Recently, the Asian shore crab *Hemigrapsus sanguineus*, has invaded much of the same region along the east coast of North America. First documented in New Jersey in

1988 (Williams and McDermott 1990), *H. sanguineus* rapidly spread into the Gulf of Maine within less than a decade (McDermott 1998a). Similarly to *C. maenas*, *H. sanguineus* also consumes large quantities of mussel prey (Ledesma and O'Connor 2001, Bourdeau and O'Connor 2003, DeGraaf and Tyrrell 2004, Brousseau and Baglivo 2005) and has been implicated in significant reductions in mussel populations within Long Island Sound (Lohrer and Whitlatch 2002b).

Though *C. maenas* is found more broadly (e.g., subtidally and in soft sediment habitats), both of these species are found abundantly in rocky intertidal areas, where extensive overlap exists in both diet and habitat use (Tyrrell and Harris 1999, Lohrer et al. 2000, Jensen et al. 2002). Similarity in resource use in turn leads to lower use of refuge habitat by *C. maenas* in areas where both crabs are found (Jensen et al. 2002), and aggressive interactions between the species while foraging (Jensen et al. 2002) that can reduce the combined impacts of these predators on shared prey (see Chapters 1-3). Additionally, negative interactions between these crabs have led to the apparent displacement of *C. maenas* from rocky intertidal habitats in southern New England (Lohrer and Whitlatch 2002a); however, *C. maenas* within the Gulf of Maine have not yet been displaced, and the two species currently coexist within rocky intertidal habitats (see Chapter 2).

In this study we examine resource use and interactions between invasive populations of *C. maenas* and *H. sanguineus* in the region where they currently overlap (central Massachusetts to central Maine). We first measure densities of both species at large scales (sites separated by 1-75 km), intermediate scales (coves within a single site separated by ≈50-100 m), and local scale (within individual 0.5 m^2 sampling quadrats) in

order to determine whether densities and distributions are consistent with previously documented trends in resource use and interactions between the species. We expect that densities of the two species will vary in relationship to each other based on different processes at each spatial scale. Specifically, crab densities at the large scale are determined mostly by patterns of larval settlement (Moksnes 2002, Thresher et al. 2003) and subsequent crab mortality (Moksnes 2004), and should display a latitudinal gradient reflecting the expansion of *H. sanguineus*' range and subsequent displacement of *C. maenas* (Lohrer and Whitlatch 2002a). Crabs move tens of meters over a single tidal cycle in response to resources availability (Brousseau et al. 2002, Moksnes 2002), and densities at intermediate scales should be positively correlated at this scale due to similar resource requirements of the two species (McDermott 1998a, Tyrrell and Harris 1999, Lohrer et al. 2000). Finally, crab densities at the local scale should reflect competitive/aggressive interactions between individual crabs, and a negative correlation is therefore expected (Jensen et al. 2002).

In addition to sampling population densities and distributions, we examined how foraging by both species is influenced by interactions between the species using both field experiments and natural crab diets throughout the region of overlap. We did this to determine whether documented negative interactions influence these species equally, or whether impacts are asymmetrical. Finally, we examine how mussel consumption influences growth rates to infer possible implications for negative interactions between the species that reduce mussel consumption.

Methods

Species Densities over Different Spatial Scales

We examined densities of both invasive predator species at three spatial scales in order to examine resource use and interactions between the species in the region of overlap. All sampling was done at moderately exposed sites characterized by extensive intertidal boulder fields. We are concerned here with interactions between crabs that potentially share the same food resources. Mussels are a preferred food item for both species (Ropes 1968, Brousseau and Baglivo 2005) and may therefore play an important role in the distribution of these species and in competitive interactions between the species (Jensen et al. 2002). We therefore report on sizes of crabs that readily consume mussels (*C. maenas* ≥ 20 mm carapace width (CW), *H. sagnuineus* ≥ 18 mm CW) (Ropes 1989).

Sampling at the three different scales was done specifically to examine the scale-specific hypotheses described above. We therefore did not use a nested sampling design that would have facilitated comparisons across scales; as such comparisons were not our purpose. Sampling at the large scale was conducted during June and July 2006 at 14 sites from central Massachusetts to central Maine (Fig. 5.1), representing the range over which *C. maenas* and *H. sanguineus* currently overlap in rocky intertidal areas. At each site we determined crab density and mussel density within 15 randomly placed 1 m^2 quadrats at approximately 0.5 m above mean low water. Sampling within each site was conducted within a 200 m region of coastline. We used separate multiple regressions for each species to examine how mean crab density was influenced across sites by mean density of heterospecific crabs, mean mussel density, and latitude. As crab densities and mussel

density were each positively correlated with latitude, we used residuals of crab and mussel densities (after accounting for latitude) as response variables in each analysis to avoid multicollinearity (Graham 2003). With this and all other multiple regression analyses presented here, final models were selected using stepwise procedure with 0.25 probability to enter the model and 0.15 probability to leave (Sokal and Rohlf 1995).

Sampling at the intermediate and local scales was conducted at Odiorne Point, NH during July 2005. This site was chosen due to accessibility and because it has a series of coves, each separated by bedrock outcroppings, which facilitated designation of separate intermediate scale sampling areas. Within 15 separate coves we sampled from 15 randomly placed quadrats (0.5 m^2) at approximately 0.5 m above mean low water. Sampling within each cove was conducted within a 5 m × 20 m area. Densities of the two crabs at the intermediate scale were determined from mean densities of each species among coves.

Within each cove we also quantified the abundance of important resources. *C. maenas* and *H. sanguineus* utilize several resources for food and shelter, including mussels (Ropes 1968, McDermott 1998b, Lohrer et al. 2000, Ledesma and O'Connor 2001, Lohrer and Whitlatch 2002b), barnacles (Rangeley and Thomas 1987, McDermott 1998b, Lohrer et al. 2000), macroalgae (Tyrrell and Harris 1999, Lohrer et al. 2000), and rocks (Ledesma and O'Connor 2001, Jensen et al. 2002). We determined the percent cover of macroalgae (*Ascophyllum nodosum*, and *Fucus* spp.) and rocks using a 100 point, 5 m × 20 m grid running parallel lengthwise to the water. We determined the density of mussels and barnacles within 6 separate 0.5 m^2 quadrats within each cove. While both of these species have specific size preferences for mussel prey (Elner and

Hughes 1978, DeGraaf and Tyrrell 2004), both are capable of consuming mussels over a wide size range (McDermott 1998b, Griffen pers obs). We therefore determined total mussel density rather than simply the density of mussels within the preferred size ranges. To assess potential aggregation of crabs across coves (i.e., at intermediate scales) to each of the resources listed above, we used separate multiple regression analyses for each species. Rocks were positively correlated across sites with mussels and macroalgae. We therefore avoided problems of multicollinearity using residuals of the less important variables as recommended by Graham (2003), and by considering rocks to be ecologically more important for *H. sanguineus* than mussels or macroalgae (Ledesma and O'Connor 2001), and the opposite for *C. maenas* (based on individual correlation coefficients of *C. maenas* to each of these variables).

Crab densities at the local scale were determined using the same data from Odiorne Point as were used for examining intermediate scales, but focusing on individual sampling quadrats rather than means from all sampling quadrates within a cove. We regressed *C. maenas* density (ln+1 transformed) against *H. sanguineus* density (ln+1 transformed) after removing quadrats where no crabs of either species were found.

Influence of Crab Density on Mussel Consumption

We examined how the density of both conspecific and heterospecific crabs influenced mussel consumption by *C. maenas* and *H. sanguineus*. To do this, we examined gut contents of several crabs of each species (14 ± 6, mean ± SD) from each of the 14 sites used in our large scale sampling described above. Crabs were collected haphazardly from the mid to lower intertidal on the same mornings that we sampled crab

density, and were then placed in 95% ethanol for later analysis. Both males and females from a range of sizes (*C. maenas* 22-65 mm CW, n=142; *H. sanguineus* 18-35 mm CW, n=171) were sampled. Because crabs forage most actively during nighttime high tides (Lindberg 1980, Willason 1981, Batie 1983, Depledge 1984, Saigusa and Kawagoye 1997) we collected crabs during ebb tides at dawn. All sites were sampled within a three week period of time to minimize seasonal differences.

Gut contents of each crab were analyzed by spreading the contents evenly over a pre-marked grid and identifying food items overlying each grid point using a dissecting microscope (Tyrrell and Harris 1999). Unidentifiable particles were counted as detritus. Percent contribution of mussels to the diet was determined by dividing the number of grid points with mussels by the sum of grid points that had any food items for each crab. This was then averaged across all crabs for each species within each site. Only crabs with guts full enough to cover 10% of the grid points were used (*C. maenas* n=88, *H. sanguineus* n=117).

We determined the importance of crab density and mussel availability for mussel consumption by *C. maenas* and *H. sanguineus* using separate multiple regression analyses for each species. We used percent contribution of mussels to the diet at each site as the response variable with mussel density, *C. maenas* density (square root transformed to equalize spacing of values along x-axis and avoid giving undue weight to values with very high crab densities), *H. sanguineus* density (square root transformed), and latitude for each site as potential explanatory variables. We also explored the possibility that any decreased mussel consumption was compensated by increasing consumption of other animal prey (barnacles, snails, amphipods, urchins). To do this we

examined the correlation between mussels and each of these other prey species found in the guts. Increasing presence of these other food items with decreasing presence of mussels would indicate compensative feeding.

Experimental Examination of Heterospecific Effects on Foraging

We experimentally examined changes in foraging by *C. maenas* and *H. sanguineus* as a result of interactions in the field by examining the amount consumed and the diet of each species when foraging separately and together. We deployed 18 cages (0.21 m^2, constructed of 1.27 cm wire mesh) at approximately 0.5-1.0 m above mean low water at Broad Cove, Isle of Shoals, located approximately 10 km off the coast of New Hampshire. Small boulders from the surrounding habitat with attached algal and faunal prey were haphazardly placed in the cages. We further supplemented each cage with 40 mussels and 10 g wet weight each of *Fucus spp.*, *Ulva intestinalis*, *Chondrus crispus*, and *Mastocarpus stellata.* An abundance of food was thus available in the cages and remained at the end of each trial. Food limitation was therefore not a factor. Crabs were starved for approximately one week before being randomly assigned to three treatments: one *H. sanguineus* only, one *C. maenas* only, and one *H. sanguineus* and one *C. maenas* together (*C. maenas*: 42.3 ± 8.8 and *H. sanguineus*: 25.9 ± 2.6 mm CW, mean ± SD). Crabs were placed inside cages and were allowed to forage for 48 h. Three trials were conducted during late July and early August 2005, yielding 18 replicates of each treatment.

Experiments were terminated during ebbing tides at dawn, and gut contents were then analyzed as previously described. We determined percent gut fullness by counting

the proportion of the grid points that were covered by food. We corrected for differences in crab size by standardizing to the largest size crab for each species within the experiment. Gut fullness for each species foraging independently was compared to gut fullness in the presence of a competitor using two-way ANOVAs with presence and absence of a competitor as a fixed factor, and trial treated as a random factor (three levels). We also determined whether each species changed the proportion of foods in their diet in the presence of a competitor by comparing the gut contents of each predator species foraging independently and in the presence of a competitor using separate MANOVAs for each species on arcsine square root transformed proportion of diet composed of the major food items (mussels, barnacles, snails, amphipods, macroalgae, and detritus).

Effect of Mussels on Crab Growth

We experimentally examined whether changes in mussel consumption affect growth rates of *C. maenas* or *H. sanguineus*. We placed individual *C. maenas* (initial CW: 20.7 ± 1.6, mean ± SD) and *H. sanguineus* (initial CW: 16.8 ± 3.7) into enclosed 500 ml plastic containers with mesh sides, suspended in a flow through aquarium at the University of New Hampshire coastal marine laboratory in Newcastle, NH.

We provided each crab with 5 g of the alga *Chondrus crispus* and one of 11 mussel abundances (<5 mm shell length): 0, 4, 8, 12, 16, 20, 24, 32, 40, 50, or 60. Each of these treatments was repeated with one male and one female of each crab species. *C. crispus* was chosen because it is abundantly found throughout the Gulf of Maine, was frequently found in guts of field captured crabs, and was favored by both crab species in

preliminary trials. Crabs ate <0.5 g day^{-1} in preliminary feeding trials (Guy and Griffen, unpublished data), thus the 5 g we used provided excess food to sustain the crabs for one week (at which time it was replenished), allowing us to examine the effects of mussel consumption on crab growth without limiting food (i.e., growth was a function of proportion of diet composed of mussels rather than total amount of food eaten). Initial carapace width was measured after one week in the lab (rather than at the start of the experiment) to ensure that any growth was due to experimental treatments rather than to food consumption in the field prior to the start of the experiment.

The experiment ran for 14 weeks from June to September 2006. Each week we assessed the number of mussels consumed and the mass of remaining algae. We then provided each crab with fresh algae and the appropriate number of mussels. We included three controls that contained only algae to assess consumption-free changes in algal mass. At the end of the 14 weeks we measured the carapace width of each crab to assess growth. Total growth was compared between the species using paired t-tests (grouped by mussel treatment). We compared the total number of mussels consumed over the duration of the experiment and the mass of algae consumed using separate ANCOVAs, with species and sex as fixed factors and mussel treatment as a covariate. We used multiple regression to compare percent change in carapace width for each species separately based on sex, initial carapace width, total algal consumption over the duration of the experiment, and total number of mussels consumed over the duration of the experiment.

Results

Species Densities over Different Spatial Scales

The correlation between the two invasive species was scale dependent. At the large scale, *C. maenas* and *H. sanguineus* showed a negative correlation in abundance across latitude. Specifically, *C. maenas* densities decreased from north to south (P=0.0004, R^2=0.66, Fig. 5.1), while *H. sanguineus* densities increased from north to south (P=0.002, Fig. 5.1) and were higher at sites with higher mussel densities (P=0.037, model R^2=0.66). However, while densities of the two species were negatively correlated across sites (R^2=0.34), after accounting for affects of latitude, the density of heterospecific crabs did not explain a significant amount of the variation in density for either species (not included in selected models at α=0.15).

In contrast, at intermediate scales (within a single site), there was a weak positive correlation in the densities of the two species (P=0.08, R^2=0.22, Fig. 5.2). Multiple regression analyses indicated that densities of the two species showed similar positive correlations to food and habitat resources across coves at Odiorne Point. Specifically, at intermediate scales *C. maenas* density increased with mussel density (P=0.0006, Fig. 5.2) and decreased with percent cover of macroalgae (P=0.03, Fig. 1B) (77% of total variance in *C. maenas* density explained by these two factors), while *H. sanguineus* densities were positively correlated with mussel densities (P=0.008, Fig. 5.2), percent boulder coverage (P=0.001, Fig. 5.2), and negatively correlated with percent cover of macroalgae (P=0.05, Fig. 5.2) (78% of total variance in *H. sanguineus* density explained by these three factors).

At the local scale at which crabs interact (within individual 0.5 m^2 sampling quadrats), a negative relationship was found between the two species (P=0.002, Fig. 5.3).

Influence of Crab Density on Mussel Consumption

Percent contribution of mussels to *C. maenas*' diet was highly variable, increasing with higher mussel density (P=0.006, Fig. 5.4) and decreasing with higher *H. sanguineus* densities (P=0.017, Fig. 5.4). Decreased mussel consumption by *C. maenas* was not compensated by increasing consumption of any other animal prey, as there was no correlation between the presence of mussels and other animal prey in *C. maenas* guts (R^2<0.001 each for barnacles, snails, amphipods, and urchins). In contrast, percent contribution of mussels to *H. sanguineus*' diet increased with higher mussel density (P=0.014, Fig. 5.4), but was not influenced by *C. maenas* density (not included in selected regression model at α=0.15). Similarly, conspecific density did not influence mussel consumption by either species. Across all sites, a greater proportion of *C. maenas* diet was composed of mussels (30 ± 8%, mean ± SE) than for *H. sanguineus* (9% ± 3%). And we found no influence of crab size on percent contribution of mussels to the diet within the ranges of crab sizes examined here for either species (P>0.20; size ranges: *C. maenas* 22-65 mm CW, *H. sanguineus* 18-35 mm CW).

Experimental Examination of Heterospecific Effects on Foraging

The presence of *H. sanguineus* strongly influenced prey consumption by *C. maenas* in our field caging experiment as evidenced by gut content analyses. While the strength of *H. sanguineus*' influence varied across trials (P=0.03), overall *C. maenas*

consumed less food when *H. sanguineus* was present ($P = 0.009$; Fig. 5.5). Additionally, *C. maenas* consumed fewer mussels and amphipods and consumed more red algae when *H. sanguineus* was present (Wilk's Lambda = 0.56, $P = 0.006$; Fig. 5.6). In contrast, *H. sanguineus* did not alter the amount of food that it consumed ($P = 0.41$; Fig. 5.5) or the content of its diet (Wilk's Lambda = 0.75, $P = 0.19$; Fig. 5.6) when *C. maenas* was present.

Effects of Mussels on Crab Growth

C. maenas consumed more mussels in our laboratory growth experiment than *H. sanguineus* (ANCOVA, P=0.007), while *H. sanguineus* consumed more algae (ANOVA, P<0.0001). Neither consumption of mussels or algae was influenced by crab sex (ANOVAs, P>0.2). Overall, *C. maenas* grew more than *H. sanguineus* during the 14 week experiment (two-sided paired t-test, P<0.0001, Fig. 5.7). Multiple regression indicated that growth for *C. maenas* increased with the number of mussels consumed (P=0.006, Fig. 5.7), and with the total amount of algae consumed (P=0.07), with greater percent change in carapace width for smaller crabs (P=0.009). For *H. sanguineus*, growth also increased with the number of mussels consumed (regression, P=0.0008, Fig. 5.7), with greater percent change in carapace width for smaller crabs (regression, P<0.0001). However, if the lowest two abundances of mussels are removed from the analyses (zero and four mussels offered per week), the positive relationship between mussel consumption and growth disappears for *H. sanguineus* (regression, P=0.18), but persists for *C. maenas* (regression, P=0.02).

Discussion

Results of our sampling studies were consistent with previously documented interactions between *C. maenas* and *H. sanguineus* and resource utilization by each species at all three spatial scales. Specifically, while sampling on the New Hampshire coast in the late 1990s and early parts of this decade found that *C. maenas* outnumbered *H. sanguineus* 10:1 (Tyrrell et al. 2006), we found that these crabs are now approximately equal in abundance on the New Hampshire coast. This fact, together with inverse densities of these species across latitudes in the southern Gulf of Maine (Fig. 5.1), is consistent with the advancing invasion of *H. sanguineus* and could also indicate further displacement of *C. maenas* from rocky intertidal areas as has been demonstrated at multiple sites further south in Long Island Sound (Lohrer and Whitlatch 2002a).

The positive correlation between these species at the intermediate scale resulted from aggregation to areas with abundant food and refuge (Fig. 5.2, Ledesma and O'Connor 2001, Moksnes 2002). And this similarity in resource use by these species (Fig. 1B, Tyrrell and Harris 1999, Lohrer et al. 2000) results in aggressive/competitive interactions between the species (Jensen et al. 2002), consistent with the negative correlation between these species on a local scale (Fig. 5.3). The shift from a positive to a negative correlation in the density of *C. maenas* and *H. sanguineus* between intermediate and local scales is consistent with theoretical predictions of species that negatively interact yet respond similarly to underlying environmental factors (Byers and Noonburg 2003). Density patterns observed here were not influenced by our choice to report only densities of large crabs, as analyses conducted with small crabs included served only to strengthen the observed trends. However, densities of large *C. maenas* in

intertidal habitats may increase at high tide relative to what we observed in our low tide sampling, as large subtidal crabs may move up with the tide to forage (Hunter and Naylor 1993).

Results of our gut content analysis on freely foraging crabs in the field and on crabs within our field experiment support that *H. sanguineus* is directly responsible for eliciting a diet shift in *C. maenas* from consuming mussels (a preferred food item in laboratory prey choice experiments, Guy and Griffen unpubl. data) to consuming more red algae (the less preferred prey item) (Fig. 5.6). Reduced mussel consumption by *C. maenas* in the presence of *H. sanguineus* may not reflect competition for a limited resource, as mussel density was high at multiple sites where *C. maenas* mussel consumption was low (Fig. 5.4). Rather, it may reflect kleptoparasitism or displacement of *C. maenas* from prey by *H. sanguineus* (Jensen et al. 2002), or may potentially reflect a 'hardwired' behavioral response to high densities of any competing individuals (Connell 1980).

Our regression analysis did not detect any effect of conspecific density on mussel consumption by *C. maenas*, and our field experiment did not include the necessary treatment to determine whether a similar diet shift occurs in the presence of a conspecific competitor. However, combined prey mortality is equally reduced because of predator interference when these two species are combined in conspecific and heterospecific pairs (see Chapters 1 and 3). Further, conspecific interference among experimentally high *C. maenas* densities greatly reduces mussel consumption (Smallegange et al. 2006) and decreases predation in general (Griffen and Delaney, In Prep). Thus the impact of *H.*

sanguineus on *C. maenas* foraging and the absence of an impact of conspecifics may simply reflect the difference in density of the two species.

Maximum *H. sanguineus* densities across our sampling sites were more than twice as high as the maximum *C. maenas* densities (Fig 5.1). And mussel consumption by *C. maenas* was particularly low at some sites where *H. sanguineus* was very abundant (Fig. 5.4), despite high mussel densities at these sites indicating that the effect of *H. sanguineus* on *C. maenas* was largely driven by these sites. However, given that *H. sanguineus* densities are frequently much higher than *C. maenas* densities within the invaded region (Fig. 5.1, and see Chapter 6), the impacts of *H. sanguineus* on *C. maenas* predation may frequently be larger than impacts of conspecifics. If this is the case, then diet changes by *C. maenas* resulting from interactions with *H. sanguineus* could potentially contribute to the replacement of *C. maenas* by *H. sanguineus* in rocky intertidal habitats. Reduced mussel consumption led to lower growth rates in *C. maenas* (Fig. 5.7), likely due to a lack of protein (Ponat and Adelung 1980). Reduced growth rates may increase mortality by increasing the time necessary to achieve a size refuge from predation/cannibalism (deRivera et al. 2005), and could also potentially decrease population growth rates by increasing time to maturity, or by decreasing size at maturity (Twombly and Burns 1996).

In addition to the negative influence of *H. sanguineus* on *C. maenas* mussel consumption and resulting growth rates, *H. sanguineus* also consumes settling *C. maenas* postlarvae (Lohrer and Whitlatch 2002a) and displaces juvenile *C. maenas* from refuge habitat under rocks (Jensen et al. 2002). The impacts of *H. sanguineus* on *C. maenas* through these combined mechanisms appear to be significant and are likely responsible

for the elimination of *C. maenas* from rocky intertidal habitat that it once inhabited in Long Island Sound (Lohrer and Whitlatch 2002a), and may also be contributing to the low *C. maenas* densities at sites with high *H. sanguineus* densities observed in our large scale sampling (southern most sites in Fig. 5.1).

In contrast, no negative impacts of *C. maenas* on *H. sanguineus* have been detected in this or previous studies. Thus, at least for several important processes (recruitment of new individuals to the population, use of refuge habitat to avoid predation threats, and energy acquisition), interactions between these species are severely lopsided, representing amensal (–/0) interactions. The extent to which these individual amensal interactions result in a population level amensal interaction between these species depends on the extent to which *H. sanguineus* benefits energetically from consumption of *C. maenas* juveniles. Yet, regardless of whether absolute interactions between these species are amensal, this study highlights that, rather than facilitation and an invasional meltdown, interactions between multiple invasive species that fill similar niches may be inhibitory, moderating their impacts on native communities.

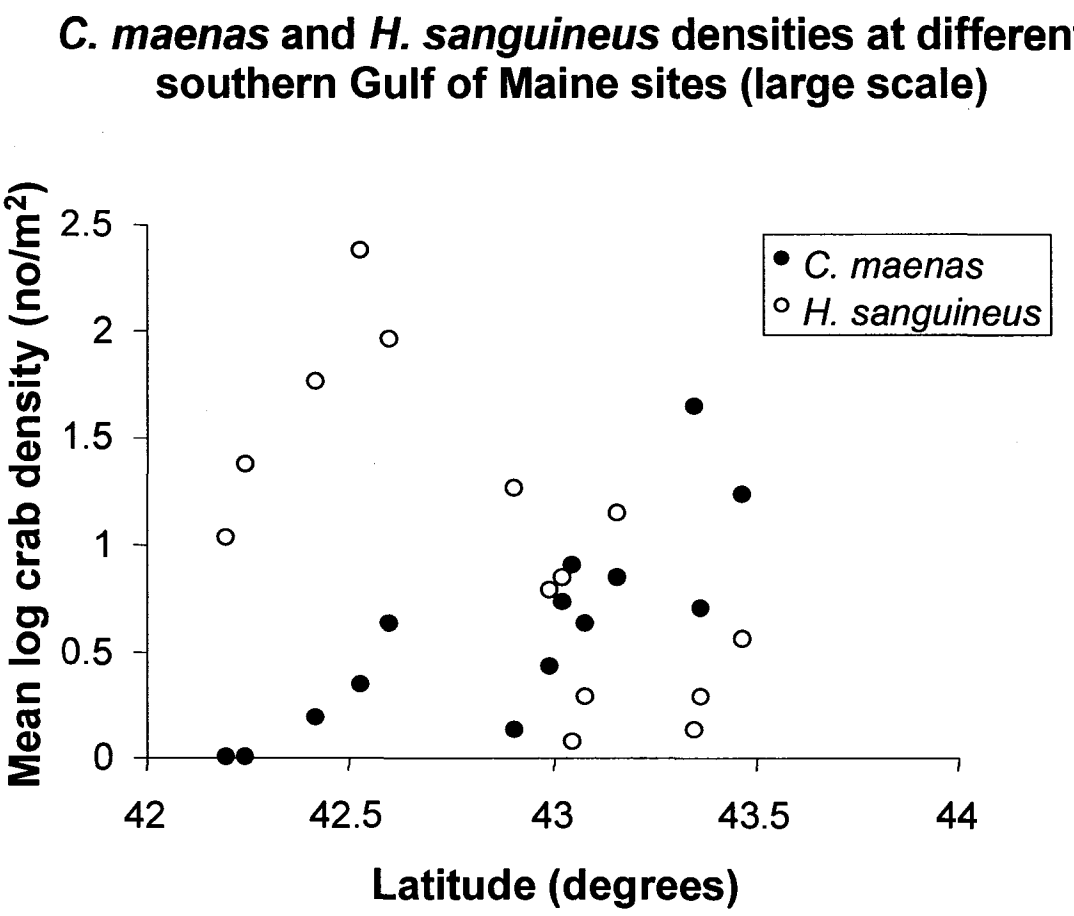

Figure 5.1 Density of large *C. maenas* and large *H. sanguineus* at 14 sites within the southern Gulf of Maine. Values are averages from 15 quadrats at each site.

C. maenas and *H. sanguineus* densities as a function of resource levels across coves at Odiorne Point, NH (intermediate scale)

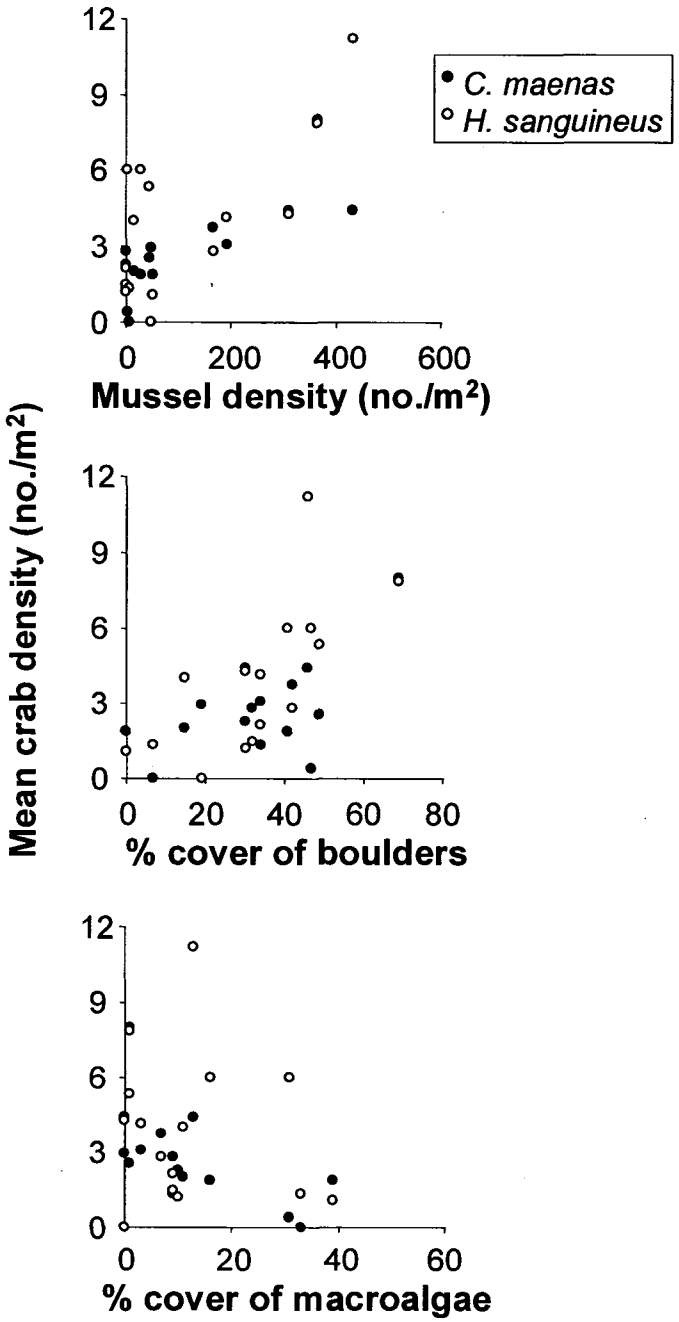

Figure 5.2 Density of large *C. maenas* and large *H. sanguineus* at intermediate scale indicating crab density in relation to mussel density, percent cover of boulders, and percent cover of macroalgae between coves separated by 50-100 m at Odiorne Point, NH. Values are averages from 15 quadrats from each cove.

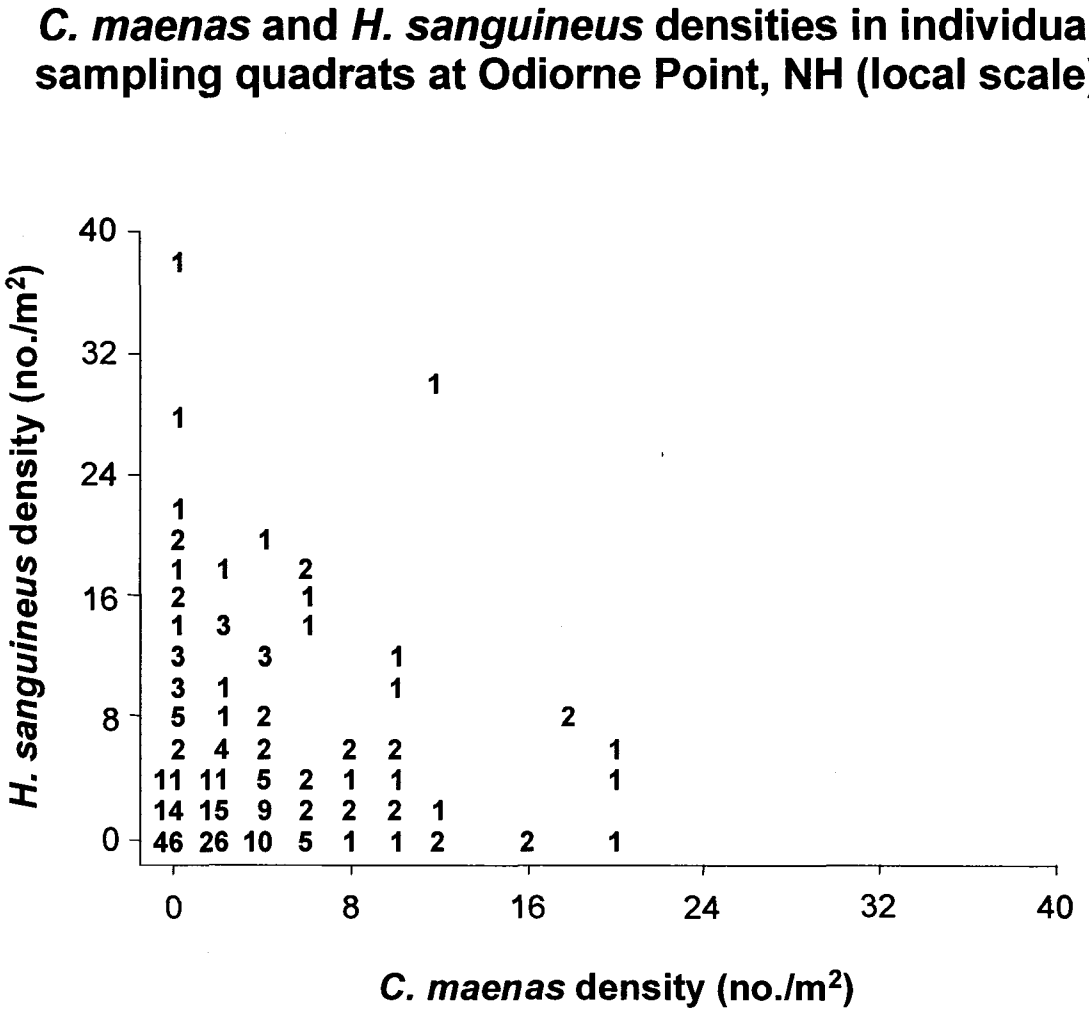

Figure 5.3 Density of large *C. maenas* and large *H. sanguineus* at local scale on which individual crabs interact. Values represent the number of individual sampling quadrats (from sampling at intermediate scales shown in Figure 5.2) with a specific density of each crab species. For example, 46 quadrats had no individuals of either species.

Effect of heterospecific crab density and mussel density on mussel consumption by *C. maenas* and *H. sanguineus*

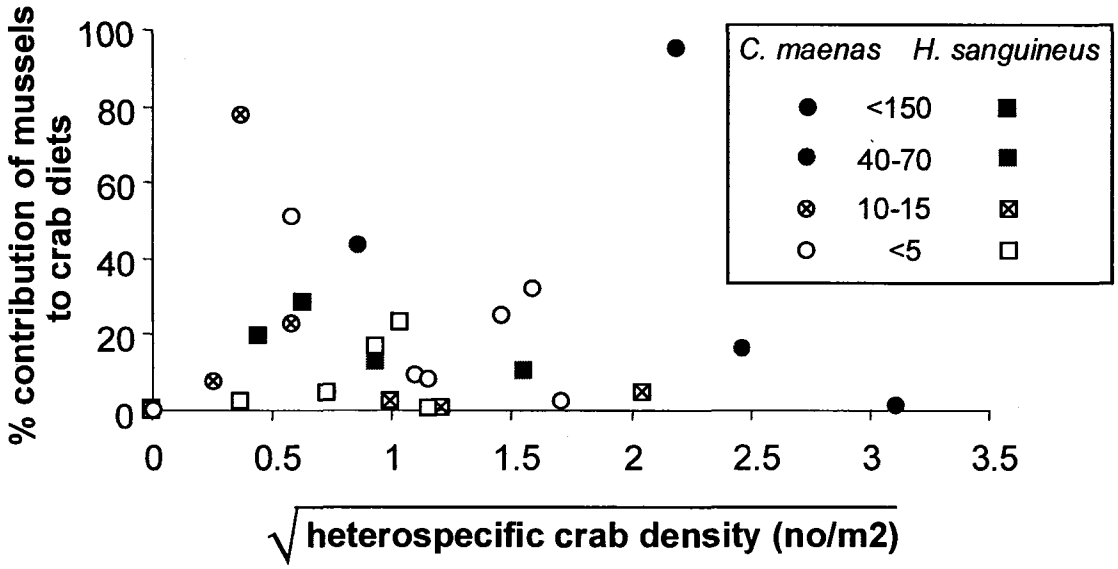

Figure 5.4 Percent contribution of mussels to diets of *C. maenas* and *H. sanguineus* at several sites within the southern Gulf of Maine as a function of heterospecific crab density and mussel density. For presentation purposes the density of mussels is divided into four categories (shown in legend as ranges of density m^{-2}), but was continuous for statistical analyses.

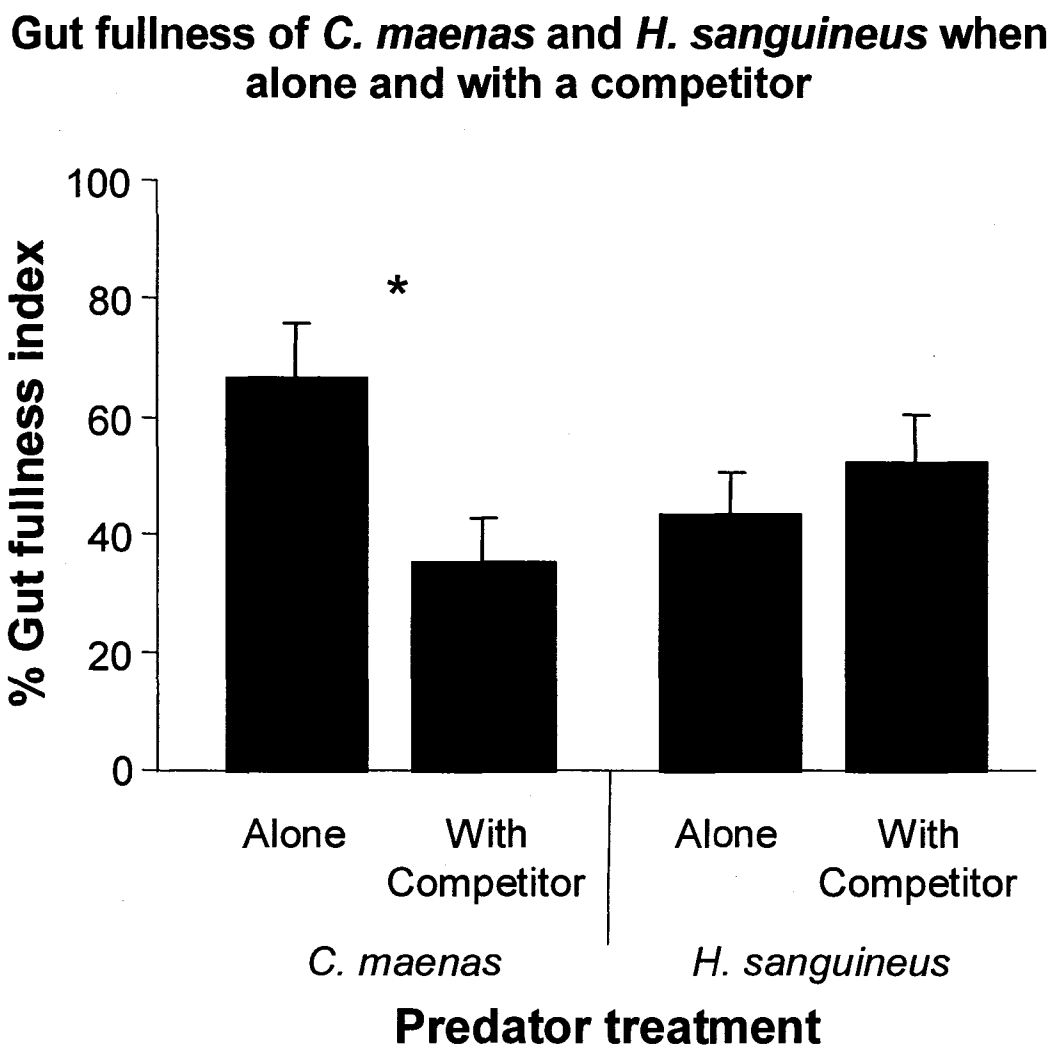

Figure 5.5 Percent gut fullness (mean ± SE, n = 18) of *C. maenas* and *H. sanguineus* guts after foraging in field cages on standardized prey community for 48 h either alone or in the presence of a heterospecific competitor. Significant differences in the absence and presence of a competitor is indicated by asterisks, where * $p < 0.01$

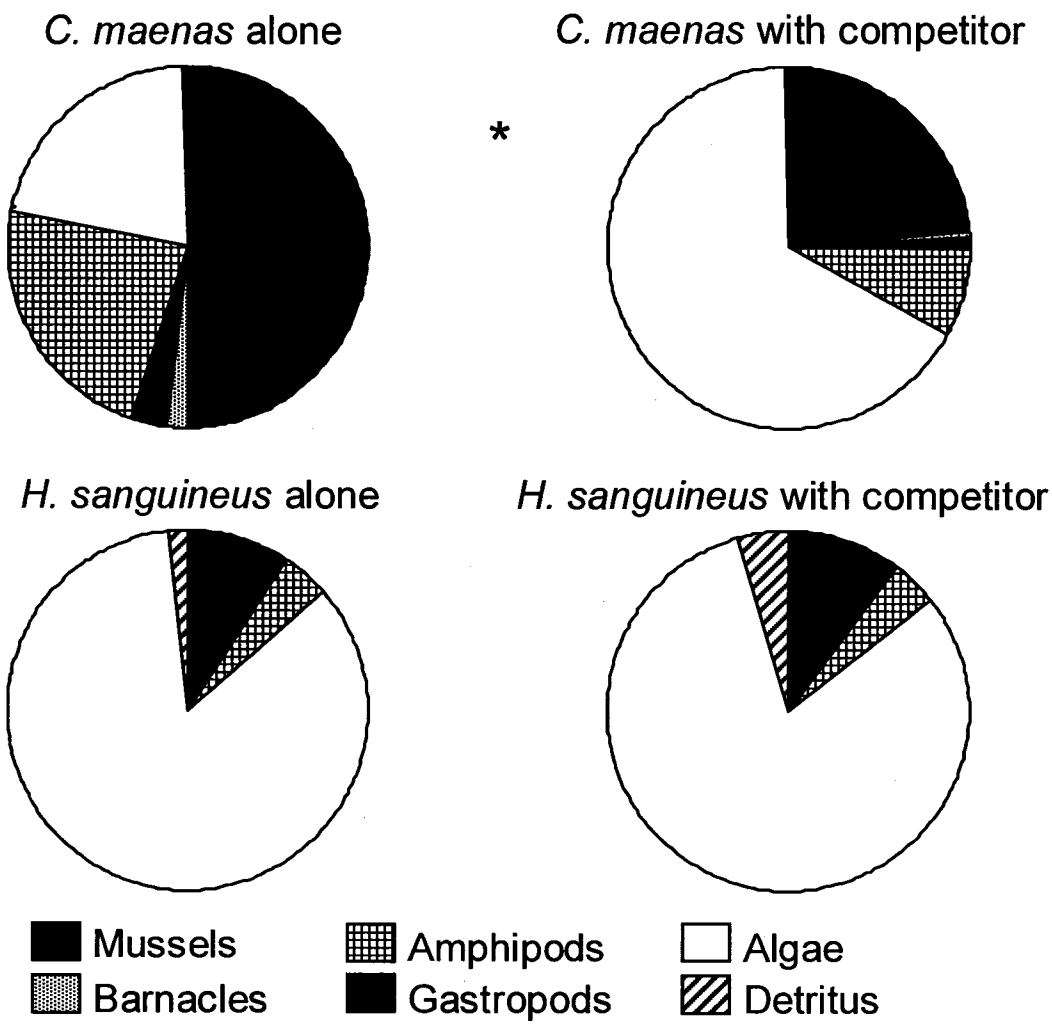

Figure 5.6 Mean proportion of food items found in guts of *C. maenas* and *H. sanguineus* after foraging in field cages on standardized prey community for 48 h either alone or in the presence of a heterospecific competitor. Significant differences in the absence and presence of a competitor is indicated by asterisks, where * $p < 0.01$

Influence of mussel consumption on growth rates of *C. maenas* and *H. sanguineus*

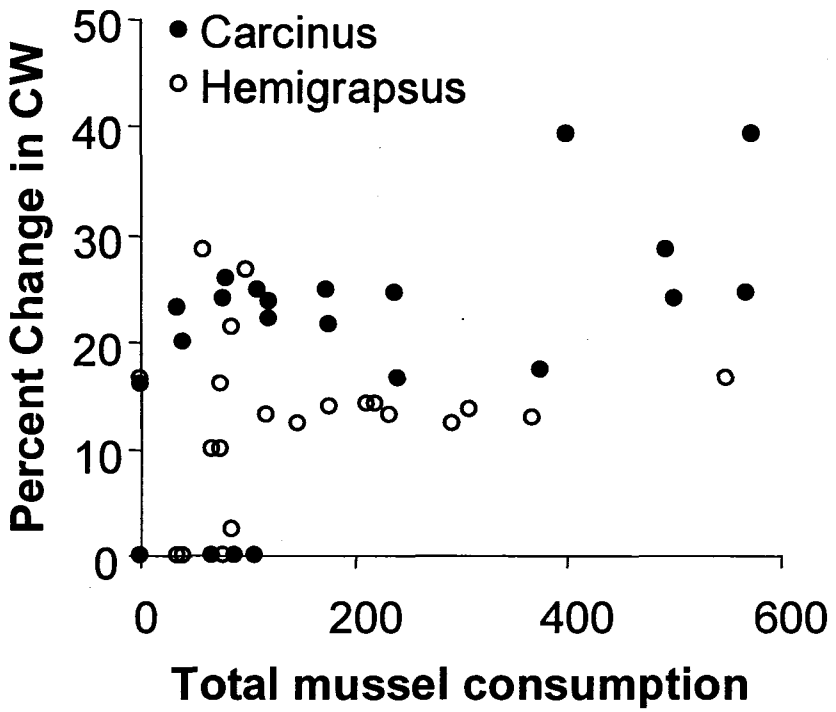

Figure 5.7 Effect on crab growth of experimentally altering the proportion of crab diet composed of mussels. Sex had no effect on growth and is therefore not distinguished here for clarity of presentation

CHAPTER 6

DIFFERENT COMMUNITY IMPACTS OF TWO INVASIVE CRABS: THE ROLES OF DENSITY, PREY RECRUITMENT, AND INDIRECT EFFECTS

Abstract

Assessing the implications of species invasion for native communities requires determining whether effects of invaders are novel, or are redundant with effects of species that are already present. Using a pair of field experiments conducted over two successive years, we examined factors that influence the community impacts of a recent predatory crab invader (*Hemigrapsus sanguineus*) and a previously established invasive crab (*Carcinus maenas*). We demonstrate that the direct and indirect impacts of both species depended on their density, temporal variation in the abundance of different prey types, and to a lesser extent on interactions between the crab species themselves. Because, *H. sanguineus* does not suppress foraging behavior by other consumers (carnivorous and herbivorous snails) to the same extent as *C. maenas* and because *H. sanguineus* achieves much higher population densities, *H. sanguineus* will exert strong impacts on native communities in areas where it displaces *C. maenas* to become the predominant predatory crab.

Introduction

Invasive species can alter species composition or richness in invaded regions by causing extinction of native species (Clavero and Garcia-Berthou 2005), replacing previously established non-native species (Lohrer and Whitlatch 2002a), or increasing local species diversity (Sax 2002, Sax and Gaines 2003). These changes in species composition or species richness may in turn have important consequences for ecosystem function (Parker et al. 1999, Hooper et al. 2005). Whether a new invader alters ecosystem function depends largely on the novelty of its effects within the invaded community (Crooks 2002). If its effects are redundant with those of species already present (*sensu* Lawton and Brown 1993), then impacts of the introduction on the wider native community may be small.

Ultimately, the level of understanding needed for many conservation goals is to assess the redundancy of invading species at the community level (Byers et al. 2002). That is, the questions of interest to ecologists are typically: what are the impacts of a new invasive species population on the native community, and how do these impacts differ from those of resident species' populations? However, with the notable exception of plant invaders, impacts of invasive species on entire invaded communities, rather than on just one or two focal native species, have rarely been quantified (Parker et al. 1999).

Impacts of an invasive species are determined by its range, abundance, and per capita effects (Parker et al. 1999). However, per capita effects are not fixed, but rather are influenced by several extrinsic and intrinsic factors. For example, resource consumption is influenced by the relative availability of alternative resources (Stephens and Krebs 1986), and by interactions with other species that use the same resources (Sih

et al. 1998). Additionally, scaling up from per capita effects to population level effects may be problematic if per capita effects scale nonlinearly, as may be the case when population density influences the importance of intraspecific interactions (e.g., Byrnes and Witman 2003), and when per capita effects are age, size, or sex specific within a demographically heterogeneous population (e.g., Bergmann and Motta 2005). Despite these complexities, species impacts are often assessed by measuring the effects of single individuals (or of several individuals of similar size, sex, etc.) on simplified communities (e.g., Rossong et al. 2006, Schooler et al. 2006).

Study System

Two invasive predatory crabs have the potential to strongly affect native communities on the east coast of North America, the European green crab *Carcinus maenas* and the Asian shore crab *Hemigrapsus sanguineus*. *C. maenas* was introduced to the western Atlantic in the mid 1800's and now ranges from Nova Scotia to Maryland (deRivera et al. 2005), where it affects the native community both through direct consumption (Glude 1955, Richards et al. 1999, Lohrer and Whitlatch 2002b, Whitlow et al. 2003) and through altering behavior and morphology of native species (Appleton and Palmer 1988, Palmer 1990, Trussell et al. 2003, Freeman and Byers 2006). The more recently introduced crab, *H. sanguineus*, was first noted in New Jersey in 1988, spread quickly, and now ranges from central Maine to North Carolina (McDermott 1998). Populations of this new invader are often very dense, and a recent survey of 30 sites throughout New England found that mean densities of *H. sanguineus* were approximately six times higher than current and historic *C. maenas* densities (Griffen and Delaney, In

Prep). Recent studies imply that *H. sanguineus* may have broad impacts on the native community (Tyrrell and Harris 1999, Ledesma and O'Connor 2001, Bourdeau and O'Connor 2003, Brousseau and Baglivo 2005), as well as large species-specific effects on bivalve prey (Lohrer and Whitlatch 2002b).

While *C. maenas* is found in a broader range of habitats, both species are found abundantly in rocky intertidal areas. Negative interactions between these species are common (Chapters 2 and 3, and Jensen et al. 2002), and the spread of dense *H. sanguineus* populations has apparently caused the disappearance of *C. maenas* from most rocky intertidal habitats in Long Island Sound (Lohrer and Whitlatch 2002a, Kraemer et al. In Press). *H. sanguineus* populations in the Gulf of Maine are also on the rise and a similar species replacement may be in progress in these northern regions (Griffen and Delaney, In Prep).

The observed replacement of *C. maenas* by *H. sanguineus* and the likelihood for continued replacement as *H. sanguineus* populations increase underscore the need to determine the relative impacts of these species on intertidal communities. Previous studies have compared the impacts of these species by examining diets using gut contents (Lohrer et al. 2000) and food preferences (Tyrrell and Harris 1999). And multiple studies have experimentally compared consumption rates on individual prey taxa (Chapter 1, and Lohrer and Whitlatch 2002b, DeGraaf and Tyrrell 2004), or have examined broader predatory impacts using small numbers of crabs of the same size and sex over short time frames (Tyrrell et al. 2006).

However, several factors not accounted for in previous studies may influence the population impacts of these species on the invaded community. First, negative

interactions between these species in areas where they still coexist can alter prey consumption (Chapters 1-5, and Jensen et al. 2002). Second, the density of each species varies widely, with consistently higher *H. sanguineus* densities in areas where it has established (Lohrer and Whitlatch 2002b, Griffen and Delaney, In Prep), and may alter population impacts via density-dependent interference (Smallegange et al. 2006) and/or cannibalism in demographically heterogeneous populations (Moksnes 2004). Third, the impacts of these species on the native prey community may be influenced by temporal variation in environmental conditions and prey availability (Elner 1980). And fourth, indirect effects as other consumers alter foraging in the presence of the invasive crabs within a larger community context (Trussell et al. 2002, 2003). We examined how each of these factors influence the overall community impacts of *C. maenas* and *H. sanguineus* using field experiments.

Methods

Experimental Design

We used two field enclosure experiments conducted in 2005 and 2006 to examine the factors that influence community impacts of two dominant intertidal invasive predators on rocky New England shores. Enclosures (0.6 × 0.45 × 0.3 m) constructed of lobster wire and lined with 0.5 cm plastic mesh were placed along a 50 m stretch of beach at approximately 0.3 m above mean low water at Odiorne Point, NH, a semi-exposed site dominated by cobble and boulders where *C. maenas* and *H. sanguineus* are found in high abundances. Five to eight small boulders (the total number varied in an attempt to

standardize cage fullness and abundance of associated prey) were placed inside of each cage. Naturally occurring flora and fauna were not removed from these boulders.

Dominant prey species that were followed in this study included three species of red algae (*Chondrus crispus*, *Mastocarpus stellatus*, and *Polysiphonia lanosa*), two groups of brown algae (*Fucus* sp. and *Ascophyllum nodosum*), the barnacle *Semibalanus balanoides*, the mussel *Mytilus edulis*, the carnivorous whelk *Nucella lapillus*, and two herbivorous snails *Littorina littorea* and *Littorina obtusata*. Both species of crab consume large quantities of mussels (Lohrer and Whitlatch 2002b). We therefore standardized the number and sizes of mussels within each cage to enable a more precise comparison of effects. Individuals of all other species were present in their naturally available densities and size ranges. While we did not count individuals of each of these other species, we standardized initial conditions between cages by placing rocks inside enclosures that were similar in their community composition based on visual inspection, a process that was greatly facilitated by the low species richness found in New England rocky intertidal sites (Menge 1976). Small, highly mobile prey that could pass through cage mesh such as amphipods and isopods were not explicitly examined in this study due to the difficulty of accurately quantifying these species. However, these are readily consumed by both crab species (Chapters 1 and 2), and likely provided an additional food source for crabs in our experiments.

Cages were deployed each year in the beginning of April and communities contained inside cages were allowed to equilibrate for six weeks prior to introducing crab predators in mid-May. Experimental treatments differed between the two years to facilitate testing different factors, and were randomly assigned to cages each year (Table

6.1). In 2005 we examined how interactions between the species influenced their overall impacts on the prey community. Four different treatments were each replicated eight times: 10 *C. maenas*, 10 *H. sanguineus*, 5 crabs of each species, and a no crab control. These densities are consistent with densities at our field site and at other sites where both species are common (Chapter 5). The substitutive experimental design mimicked densities of *C. maenas* and *H. sanguineus* at Odiorne Point that are negatively correlated at the local scale on which crabs interact (i.e., the scale of our experimental cages) (Chapter 5).

In 2006 we examined the influence of conspecific predator density on community impacts of *C. maenas* and *H. sanguineus*. Treatments including 10, 20, and 40 individuals of each species alone were each replicated four times. A no crab control was replicated three times. The lowest density was chosen to represent *C. maenas*' carrying capacity (Lohrer and Whitlatch 2002b) and the highest density was chosen to roughly approximate *H. sanguineus*' carrying capacity (Kraemer et al. In Press), allowing for an explicit comparison of the population level effects of these two species. This four-fold difference is less than the six-fold differences in mean densities throughout their invaded ranges (Griffen and Delaney, In Prep), and thus is a conservative representation of natural differences in population sizes of these two species. We included the intermediate density to determine whether effects of each species scaled linearly with density. While treatments with 20 and 40 *C. maenas* exceed natural densities of this species, our press experimental design maintained these high densities, allowing comparison between the species without confounding density differences. Annual variation in impacts and in

redundancy due to temporal changes in the prey base was assessed by comparing between the single-species treatments with 10 individuals in both years.

All crabs were collected by hand on site at Odiorne Point. We used a 50:50 sex ratio and a range of sizes of both species in each treatment, mimicking population demographics at our field site. Specifically, we used a 7:2:1 ratio of small:medium:large crabs, where small, medium, and large *C. maenas* were 12-18, 20-25, and 40-55 mm carapace width (CW), respectively, and *H. sanguineus* were 12-15, 20-25, and 29-34 mm CW, respectively.

At monthly intervals, the contents of each cage were monitored and missing crabs were replaced. This monthly interval was chosen as a compromise between maintaining experimental crab densities and minimizing disturbance to the experiments. Missing crabs resulted from cannibalism and intraguild predation rather than escape. This was verified by the presence of carapace fragments found inside of enclosures and was further corroborated by comparing the proportion of small crabs missing across crab densities in 2006 (see below), as cannibalism results in proportionally greater mortality with increasing predator density (Moksnes 2004).

During the 2006 experiment we also mimicked the availability of allocthanous drift algae as a potential food source by placing 20 g of *Chondrus crispus* (the most abundant species of drift algae at our field site) in each cage at monthly intervals. Remaining *C. crispus* from the prior addition was subsequently removed and replaced with fresh algae at each monthly maintenance period. We included drift algae because it may reduce impacts on the intertidal community by providing an alternative food for

crabs. However, because it is allocthanous rather than part of the permanent intertidal community, we did not include it in our analyses.

The experiment was terminated each year in mid-October. The experimental duration (May-October) thus encapsulated the portion of the year when active foraging by these species is greatest (Elner 1980). We collected the contents of each cage, including all flora, fauna, and shell fragments. In the laboratory, the number of each species of animal was assessed (live and dead). The number of mussels consumed by the predatory whelk *Nucella lapillus* was assessed by counting the number of mussel shells with characteristic drill holes. Herbivorous and carnivorous snails were enumerated in large and small categories, with the distinction between sizes set by the ability to pass through the 0.5 cm mesh used on experimental cages. Algae were separated by species and the wet weight determined. The abundance of live barnacles, empty barnacle tests (indicating likely consumption by *N. lapillus*), mussel recruits (which settled in July-August of each year and were distinguished from initial mussels by their small size, <1mm), and fucoid algae recruits inside each cage were determined by counting the number within 156 cm^2 quadrats placed on each of five separate boulders (at the site of highest barnacle density on each boulder).

Statistical Analyses of Overall Impacts on the Prey Community

Our primary goal was to examine factors that influence the overall impacts of *C. maenas* and *H. sanguineus* at the community level. We therefore analyzed the data from each year using MANOVAs combined with planned linear contrasts (detailed below) to examine the impacts of different predator treatments across all prey types (using red

algae, brown algae, mussels [log transformed], barnacles, *L. littorea*, *L. obtusata*, and *N. lapillus* as response variables). When these whole-community analyses indicated a significant difference in the impacts of the two species, we then used post hoc comparisons to examine the impacts of specific predator treatments on each prey type individually.

In 2005 we used a one-way MANOVA with predator treatment as a fixed factor (four levels: *C. maenas* only, *H. sanguineus* only, both species together, no-crab control) to compare the impacts of the two species, both when they foraged alone and when they foraged together. This was followed by three planned linear contrasts: *C. maenas* vs. *H. sanguineus*, *C. maenas* vs. both species together, and *H. sanguineus* vs. both species together. Because these analyses indicated that community impacts differed across treatments, we used post hoc ANOVAs and Tukey's tests to compare the difference in each prey type individually across the three predator treatments.

In 2006 we used a two-way MANOVA with predator species (two levels) and predator density (four levels) as fixed factors. This was followed by post hoc individual two-way ANOVAs (with the same factors) for each prey type. The treatments used also allowed us to examine the overall impacts of *C. maenas* and *H. sanguineus* while accounting for natural differences in equilibrium population size. We therefore followed each ANOVA with planned linear contrasts to compare the effects of 10 *C. maenas* and 40 *H. sanguineus* on each prey type.

We examined how changes in the prey base across years influenced the impacts of these species using data from both years when 10 individuals of either species foraged alone. We used a two-way MANOVA with predator species and year (each with two

levels) as fixed factors. This was followed by planned linear contrasts to compare redundancy in the overall impacts of the two species within each year.

We also compared the importance of cannibalism for each species at different densities using ANOVA on mean percent monthly mortality of crabs in 2006, with species and density as fixed factors. In addition, we compared the importance of cannibalism between years using data from both years when 10 individuals of either species foraged alone. We used a two-way ANOVA with predator species and year as fixed factors.

Statistical Analyses of Indirect Effects

Our study system allowed us to examine the contribution of the indirect effects of these predators to their overall impacts on the prey community within our experiments. Several indirect effects potentially occur within our system, although the number of important pathways is limited by the relatively low species richness of the Gulf of Maine intertidal. We focus here on indirect effects that have previously been documented for *C. maenas* or that are likely important given the diet preferences of these crabs. Specifically, we examine how each crab influences food consumption by carnivorous snails (Trussell et al. 2002, 2003), and facilitation of mussel settlement and fucoid establishment by barnacles (Lubchenco 1983, Navarrete and Castilla 1990, Kawai and Tokeshi 2004). Understanding the relative strengths of indirect effects of *C. maenas* and *H. sanguineus* may help to mechanistically explain differences in the overall community-level impacts of these species.

Using data from both experimental years, we examined the influence of the two crab species on mussel and barnacle consumption by the carnivorous whelk *N. lapillus* by quantifying drill holes in mussel shells and empty barnacle tests that it leaves (in contrast, crab predation on these species results in chipped mussel shells and removal of the entire barnacle from rock surfaces). We made comparisons between three treatments only: 10 *C. maenas*, 10 *H. sanguineus*, and the no-crab controls. We compared the number of drilled mussels and empty barnacle tests (both log transformed) using separate ANCOVAs with predator treatment and year as the main factors and number of *N. lapillus* in each cage as a covariate. Significant interaction terms of main factor effects were followed by Tukey's test to examine specific differences between predator treatments across the two years.

The presence of barnacles can enhance mussel recruitment by providing complex surface areas for attachment of settling individuals.(Navarrete and Castilla 1990) and can enhance establishment of fucoid algae through inhibiting snail herbivory on new recruits (Lubchenco 1983). We examined the importance of barnacle density for recruitment of mussels (log transformed) during our 2005 experiment both inside experimental cages (using ANCOVA with predator treatment as a main factor and barnacle density as a covariate) and on ambient rocks surrounding our experimental cages (using regression). Similarly we examined the importance of barnacle density for establishment of new fucoids (log transformed) in 2005 using ANCOVA with predator treatment as a main factor and barnacle density as a covariate.

Results

Species Interactions and Community Impacts

Community impacts in the 2005 experiment varied across predator treatments (MANOVA, Table 6.2A, Fig. 6.1). Specifically, the two predator species differed from each other in their overall community impacts when each foraged separately, and combined effects of the two species foraging together were similar to when *C. maenas* foraged alone, but were different from when *H. sanguineus* foraged alone (planned linear contrasts, Table 6.2B, Fig. 6.1). However, impacts of each predator combination differed by prey type. Impacts of *H. sanguineus* alone were weaker than of *C. maenas* or both predators together on mussels and herbivorous snails, and when both predators foraged together there was a trend towards weaker impacts on barnacles (survival increased by ≈40%) and brown algae (survival increased by ≈30%, though the increase was not significant) than when either species foraged alone (ANOVAs and Tukey's tests, Table 6.2C, Fig. 6.1).

Population Density and Community Impacts

The impacts of both species in the 2006 experiment differed with predator density, though the effect of predator density on prey was weaker than expected (MANOVA, Table 6.3A, Fig. 6.1). When impacts on individual prey types were examined rather than effects across the entire community, greater impacts at higher predator densities were only seen in the most abundant (red and brown algae) and most preferred prey (mussels and to a lesser extent barnacles) (ANOVAs, Table 6.3B, Fig.

6.1). In addition, while impacts of the two predators on most prey types were similar, *C. maenas* had a greater positive impact on brown algae (ANOVA, Table 6.3B, Fig. 6.1).

When approximate equilibrium densities of the two species were compared (10 *C. maenas* vs. 40 *H. sanguineus*), *H. sanguineus* had a 30-50% larger impact across the entire prey community than *C. maenas* (Fig. 6.1). However, due to low replication and high variability within treatments, our analyses had low power to detect a difference between the two species (mean power across all prey types=0.29), and a significant difference was detected only for brown algae (Linear contrasts, Table 6.3B).

Prey Variability and Community Impacts

Prey communities differed between years in the absence of predators, largely due to greater barnacle recruitment (before the experiment started) and mussel recruitment (during the experiment) in 2005 (Fig. 6.1), and greater amounts of algae in 2006 (largely due to our supplemental addition of drift algae). Impacts of both predator species were generally largest on the most abundant prey types each year. For example, effects of both species (but especially of the more carnivorous *C. maenas*) were greatest on barnacles, mussels, and snails in 2005 when these prey were abundant (Fig. 6.1). In 2006, *H. sanguineus* had greater impacts on the more abundant algae than *C. maenas* (Fig. 6.1). Overall community impacts of 10 *C. maenas* were stronger than impacts of 10 *H. sanguineus* in 2005 (planned linear contrast, Table 6.2B), but not in 2006 (planned linear contrast, Table 6.3B). However, this increase in redundancy between the crab species in 2006 was not systematic across all prey types, with the crabs becoming more similar in

their effects on mussels and herbivorous snails in 2006, but less so for some species like brown algae.

Cannibalism was an important factor causing high levels of mortality among the small size class of crabs for both species in our experiments, and became stronger for both species as predator densities increased (ANOVA, density $F_{2,23}$=5.92, P=0.02, species×density $F_{2,23}$=0.05, P=0.83). Across all densities, cannibalism was 13% stronger for *C. maenas* than *H. sanguineus* in 2006, though this difference was not significant (ANOVA, species $F_{1,23}$=1.25, P=0.28). Further comparison only at similar densities of 10 crabs per cage across years indicated that cannibalism among *C. maenas* remained consistently high over both years at approximately 40% mortality each month, while cannibalism among *H. sanguineus* increased from 11% per month in 2005 to 33% per month in 2006 when other animal prey were less available (ANOVA, species $F_{1,24}$=12.45, P=0.002, species×year $F_{1,24}$=4.44, P=0.047).

Indirect Effects

While indirect effects occurred when both species were present, they played a greater role when *C. maenas* was present. The size distribution and abundance of *N. lapillus* differed between years and across experimental treatments. In 2005, most *N. lapillus* were small (i.e., they could pass through cage mesh) and there were many more individuals found in control cages than in cages with either crab species. In 2006, most *N. lapillus* were large (i.e., they could not pass through cage mesh) and were found in similarly low numbers in all cages (Fig. 6.2A). Despite large differences in the number of *N. lapillus* between cages, barnacle mortality from *N. lapillus* predation was

independent of the number of *N. lapillus* present (ANCOVA, covariate, $F_{1,28}$=1.72, P=0.20). Rather, barnacle consumption by *N. lapillus* in 2005 decreased in response to both predator species, though more so with *C. maenas*, while barnacle consumption by *N. lapillus* in 2006 was similarly low across all treatments (ANCOVA predator treatment×year, $F_{2,28}$=3.24, P=0.05, followed by Tukey's test, Fig. 6.2B). In contrast, mussel consumption by *N. lapillus* did increase with *N. lapillus* abundance (ANCOVA, covariate, $F_{1,28}$=4.91, P=0.04). Further, mussel consumption by *N. lapillus* was only influenced by *C. maenas* in 2005, and neither crab in 2006 (ANCOVA predator treatment×year, $F_{2,28}$=3.31, P=0.05, Fig. 6.2C).

While both crab species decreased barnacle consumption by *N. lapillus*, both also heavily consumed barnacles themselves and thus had an indirect negative impact on mussels and fucoids that settle on and around barnacle tests. Specifically, predator treatment had no influence on mussel settlement inside experimental cages in 2005, presumably because mussels were too small to eat (main effect of ANCOVA, $F_{3,27}$=0.88, P=0.46), except through differentially consuming barnacles and thus altering barnacle density (covariate in ANCOVA, $F_{1,27}$=8.93, P=0.006). (Effects of barnacle density on log mussel recruitment inside cages were even stronger when pooling data over both years, highlighting the importance of this relationship). An identical positive correlation between barnacle density and mussel recruitment was also observed on ambient rocks surrounding our experimental cages in 2005 (regression, $F_{1,37}$=121.07, R^2=0.77, P<0.0001). The number of fucoid recruits increased with barnacle density (covariate in ANCOVA, $F_{1,27}$=4.76, P=0.04), and was further influenced by crab predators (main effect of ANCOVA, $F_{3,27}$=3.68, P=0.02). Relative to controls, the mean number of

fucoid recruits decreased (whether through direct consumption or indirectly through removal of barnacles) by 80% in *C. maenas* cages, and by >99% in cages with *H. sanguineus*.

Discussion

We found that the overall impacts of *C. maenas* and *H. sanguineus* differed between years and were generally greatest on the most abundant prey types (Fig. 6.1). In addition, the relative impacts of these species differed between years, with more redundancy in 2006 than 2005 (Fig. 6.1, Table 6.4). These differences in impacts and in redundancy between years were due largely to differences between years in the prey community and resulting changes in indirect effects. For example, *C. maenas* greatly reduced predation by *N. lapillus* on barnacles and mussels, consistent with previous reports (Trussell et al. 2003, Trussell et al. 2006). *H. sanguineus* also reduced *N. lapillus* predation on barnacles, though its effect was weaker; and *H. sanguineus* did not reduce *N. lapillus* predation on mussels (Fig. 6.2). However, these trait-mediated indirect effects were only apparent in 2005 when the majority of *N. lapillus* were small, and thus more vulnerable to crab predation.

While both crabs had positive indirect effects on barnacle survival, these were overshadowed by strong direct negative effects of direct barnacle consumption. This was especially true of *H. sanguineus* at high densities (Fig. 6.1). Low barnacle densities in turn reduce mussel recruitment by limiting settlement sites (this study and Navarrete and Castilla 1990). Heavy consumption of barnacles by dense *H. sanguineus* populations has also been reported in other parts of *H. sanguineus'* invaded range (Lohrer et al. 2000).

The indirect negative effect of barnacle removal on mussel recruitment could therefore be partially responsible for the large decreases in juvenile mussels in intertidal regions where *H. sanguineus* has become very abundant, effects that have previously been attributed solely to direct mussel consumption by *H. sanguineus*.

Differences between years in the predominant size of herbivorous snails (*L. littorea* and *L. obtusata*) are likely responsible for the greater impacts of *C. maenas* than *H. sanguineus* on these snails in 2005, but not in 2006 (Fig. 6.1). In 2005, small snails that could migrate through cage walls were four times more abundant than large snails in control cages. *C. maenas* reduced the abundance of these small snails (whether through predation or by eliciting emigration from cages) more than *H. sanguineus*, resulting in different snail abundances between predator species in 2005 (Fig. 6.1). In contrast, few small snails existed across all cage in 2006, and large snails that could not emigrate from cages were four times more abundant than small snails. Predation was low on these large snails, as evidenced by few shell fragments in all cages, resulting in 2006 snail abundances in predator treatments that were similar to controls (Fig. 6.1). Thus, small snails seem to be the only size class appreciably affected by crab predators, and 2005 was the only year that small snails were abundant enough for crabs to exert a detectable influence. In 2006, due to the paucity of small snails, neither crab species significantly affected snail abundance, regardless of crab density (Fig. 6.1, Table 6.3).

In contrast to animal prey with clear forensic evidence, consumption of algae in our experiments cannot definitively be attributed to specific consumers; however, differences in food preferences may provide some guidance. Both crab species overwhelmingly preferred *C. crispus* and *M. stellatus* (which comprised ≈95% of red

algae in our experiments) over brown algae in laboratory feeding trials (Griffen, unpubl. data). In contrast, both *L. littorea* and *L. obtusata* (the only herbivorous snail in our cages) prefer brown algae (Lubchenco 1978, Dudgeon et al. 1999). Consumption of red algae can therefore be attributed to crabs and/or amphipods and isopods which were not explicitly examined here. Crab consumption of brown algae in 2006 may have been reduced by our supplemental addition of red "drift" algae. At the same time, the presence of crabs may have caused herbivorous snails to reduce foraging, as has previously been shown for *L. littorea* foraging in the presence of *C. maenas* (Trussell et al. 2002, 2003). Thus, a combination of supplementing crab diets with drift algae, together with reduced foraging by snails in the presence of crab predators (particularly *C. maenas*), may help explain high survival of brown algae in our 2006 experiment, and the predominance of brown algae in New England rocky intertidal areas.

The positive indirect effects outlined above on survival of barnacles, mussels, and algae through changes in carnivorous and herbivorous snail behavior occurred in the presence of both crab species, but were generally stronger when *C. maenas* was present. At the same time, negative indirect effects shown above on fucoid establishment through changes in barnacle density, were also present with both crabs, but were stronger in the presence of *H. sanguineus*.

Lower overall impacts of crab predation in 2006 were likely due in part to low recruitment of favored prey (Fig. 6.1). This overall weaker impact in 2006, the year we examined the influence of crab density, may have contributed to the less than expected increase in community impacts of both species with increasing crab density (Fig. 6.1, Table 6.3). Differences in the densities of *C. maenas* and *H. sanguineus* are frequently

larger than the four-fold difference between our high and low densities here (Lohrer and Whitlatch 2002a, b, Griffen and Delaney, In Prep). Smaller than expected changes in the impacts of these species with increasing density and natural differences in ambient population densities may both be explained by predator interference and cannibalism. Predator interference increases with predator density, reducing per capita effects and indirectly limiting population size by altering resource consumption (Arditi et al. 2004). Predator interference is stronger among *C. maenas* than *H. sanguineus* (Griffen and Delaney, In Prep). This likely explains why higher individual consumption rates for *C. maenas* than for *H. sanguineus* that have previously been reported (Chapters 1 and 3, and Lohrer and Whitlatch 2002b) did not translate into higher impacts of *C. maenas* in our experiments as multiple individuals all foraged together (Fig. 6.1). Furthermore, cannibalism also increases with predator density and was consistently strong for *C. maenas*, thus reducing the time averaged density differences between our treatments, and directly regulating the size of natural populations (Moksnes 2004).

Though effects of increasing predator density were smaller and more variable than expected, effects of 40 *H. sanguineus* were 30-50% stronger than effects of 10 *C. maenas* across all prey types. Together, results here suggest that *H. sanguineus* has stronger population level impacts on the invaded community due to higher population densities that have stronger direct trophic effects across the entire prey community, and weaker positive indirect effects and stronger negative indirect effects on barnacles, mussels, and algae. Reduced abundance of these important primary space holding species may likely have further trickle down effects, as each is known to enhance recruitment and survival of mobile community members (Bertness et al. 1999,

McKindsey and Bourget 2001). Differences in population level effects of *C. maenas* and *H. sanguineus* (including contributions of direct and indirect effects) are highlighted in Figure 6.3.

Figure 6.3 provides a snapshot of the relative impacts of *C. maenas* and *H. sanguineus* in one year, under one set of prey conditions. While the general trend indicated in Figure 6.3 is likely to be constant, impacts on specific prey types will vary with temporal differences in the prey base and with further differences in population densities. For example, had we made a similar comparison across densities in 2005 when barnacle and mussel recruitment was higher, effects of both species on barnacles may have been greater, with correspondingly greater indirect effects on mussels, and brown algae. Additionally, because of a larger proportion of small snails in 2005, effects of *C. maenas* would have been greater on snails, though the relative importance of different densities of the two predators on small snails is uncertain. Additionally, while our study represents a substantial improvement over previous studies conducted over short time scales, there may still be important differences between these species that are expressed over longer time scales than those examined here. For example, non-significant differences in effects of the two predator species on algal biomass or snail abundance over a single "foraging season" observed here could accumulate over multiple years, resulting in important differences. Nevertheless, we believe we have captured a fairly robust picture of the relative effects of the two species at equilibrium densities.

C. maenas foraging is altered as a result of interference from *H. sanguineus* in areas where the two species coexist (Chapter 5, and Jensen et al. 2002), and this can result in greater prey survival when the two species forage together experimentally on

isolated prey species (Chapters 1-3). When crabs were placed together during our 2005 experiment, in a community context where many prey types were available to them, only survival of barnacles and brown algae modestly increased (Fig. 6.1). Thus, while some prey species benefit when the two predators coexist, interference between *C. maenas* and *H. sanguineus* does not appear to convey widespread benefits for prey survival throughout the prey community.

Conclusions

Our study demonstrates that direct and indirect effects of *C. maenas* and *H. sanguineus* on invaded prey communities are influenced by temporal variability in the prey community, by predator density, and to a lesser extent by interactions between the species. We also found that the strength of important trait mediated and density mediated indirect effects are very different in the presence of each species. Our findings suggest that *H. sanguineus* will have larger impacts than *C. maenas* due to a combination of high population densities that yield strong direct negative effects across the entire prey community, and weaker positive indirect effects and stronger negative indirect effects on primary space holding barnacles, mussels, and algae.

Table 6.1 Experimental designs used in different years to examine the impacts of predation by *Carcinus maenas* (CM) and *Hemigrapsus sanguineus* (HS). Experiments ran from beginning of April to mid October each year within field enclosure cages (0.6 × 0.45 × 0.3 m).

Year	Treatments (no. per cage)	# Reps.	Addition of drift algae?
2005	10 CM, 10 HS, 5 CM + 5 HS, None	8	No
2006	10 CM, 20 CM, 40 CM, 10 HS, 20 HS, 40 HS, None	4*	Yes

* except control treatment, which was replicated 3 times

Table 6.2 Statistical results for comparing the impacts of *C. maenas* and *H. sanguineus* alone and together on the prey community in 2005.

A) MANOVA – overall community impacts

Test	Wilks' λ	d.f.*	Approx. *F*	*P*
Whole model	0.068	21,63.7	4.58	<0.0001

B) Planned linear contrasts

Contrast	d.f.*	*F*	*P*
C. maenas vs. *H. sanguineus*	7,22	3.38	0.02
C. maenas vs. both species together	7,22	1.45	0.24
H. sanguineus vs. both species together	7,22	2.80	0.03

C) ANOVAs – impacts on individual prey types

Prey type	d.f.	*F*	*P*	Tukey's**
N. lapillus	2,21	2.43	0.09	NA
L. littorea	2,21	3.83	0.04	$C^{a}>B^{ab}>H^{b}$
L. obtusata	2,21	8.90	0.002	$B^{a}>C^{a}>H^{b}$
Barnacles	2,21	3.31	0.06	$C^{a}>H^{ab}>B^{b}$
Mussels	2,21	10.12	0.0008	$C^{a}>B^{a}>H^{b}$
Red algae	2,21	0.37	0.70	NA
Brown algae	2,21	0.68	0.52	NA

*numerator,denominator d.f.

**C=*C. maenas*, H=*H. sanguineus*, B=Both species together, NA=Tukey's test not conducted because of nonsignificant difference in ANOVA. Lowercase superscript letters indicate statistically similar treatments.

Table 6.3 Analysis of 2006 experiment examining the influence of predator density on the community impacts of *C. maenas* and *H. sanguineus* (MANOVA and ANOVAs), and examining the population level redundancy of these species (linear contrasts).

A) MANOVA – influence of density on overall community impacts

Test	Wilks' λ	d.f.*	Approx. *F*	*P*
Whole model	0.015	49,70.4	1.86	0.008
Predator density	0.088	21,37.9	2.40	0.009
Predator species	1.723	7,13	3.20	0.03
Predator density×predator species	0.161	21,37.9	1.60	0.10

B) ANOVAs – influence of density on individual prey types

Model	d.f.	*F*	*P*	Linear contrast 10C vs. 40H**
N. lappilus				
Predator density	3,19	2.56	0.09	
Predator species	1,19	5.16	0.03	
Predator density×predator species	3,19	2.12	0.13	*P*=0.47
L. littorea				
Predator density	3,19	1.30	0.30	
Predator species	1,19	0.06	0.82	
Predator density×predator species	3,19	1.30	0.30	*P*=0.24
L. obtusata				
Predator density	3,19	1.08	0.38	
Predator species	1,19	0.41	0.53	
Predator density×predator species	3,19	1.14	0.36	*P*=0.42
Barnacles				
Predator density	3,19	2.41	0.10	
Predator species	1,19	0.01	0.93	
Predator density×predator species	3,19	0.70	0.56	*P*=0.17
Mussels				
Predator density	3,19	12.17	<0.001	
Predator species	1,19	1.37	0.26	
Predator density×predator species	3,19	4.56	0.01	*P*=0.58
Red algae				
Predator density	3,19	8.33	0.001	
Predator species	1,19	5.39	0.03	
Predator density×predator species	3,19	5.87	0.005	*P*=0.12
Brown algae				
Predator density	3,19	4.15	0.02	
Predator species	1,19	7.06	0.02	
Predator density×predator species	3,19	0.82	0.50	*P*=0.005

*numerator,denominator d.f.

**C=*C. maenas*, H=*H. sanguineus*

Table 6.4 Community impacts of 10 *C. maenas* and 10 *H. sanguineus* across years with different prey bases.

A) MANOVA – overall community impacts

Test	Wilks' λ	d.f.*	Approx. *F*	*P*
Whole model	0.039	21,40.8	4.05	<0.0001
Predator species	0.876	7,14	1.75	0.18
Year	6.677	7,14	13.35	<0.0001
Predator species×year	0.647	7,14	1.29	0.32

B) Planned linear contrasts – compared species within each year

Contrast	d.f.*	*F*	*P*
2005	7,14	3.10	0.03
2006	7,14	0.67	0.64

*numerator,denominator d.f.

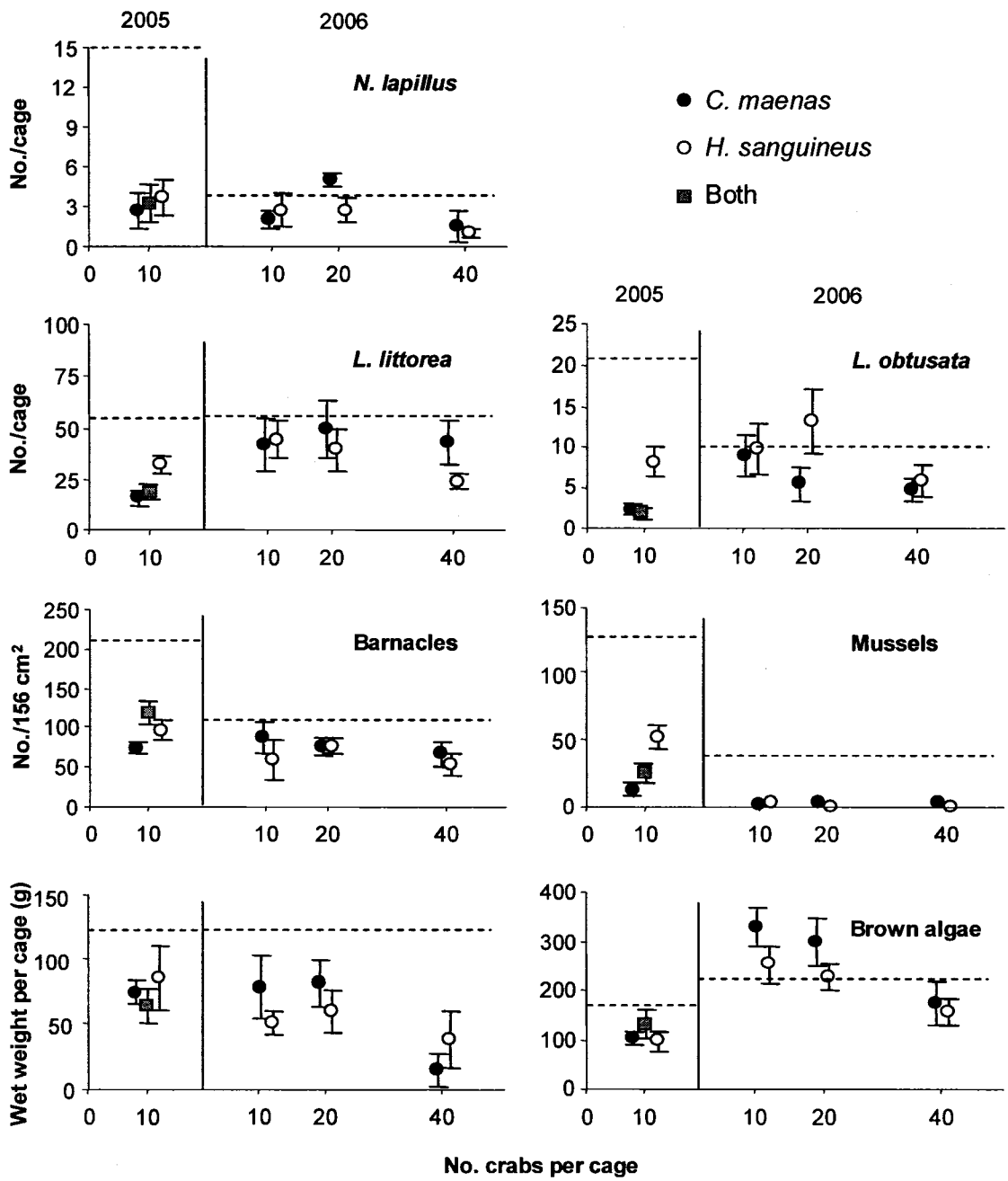

Figure 6.1 Survival of different prey types in 2005 (left side of vertical bar, mean ± SE, n=8) and 2006 (right side of vertical bar, mean ± SE, n=4). Horizontal dashed line represents mean value in no-crab control cages each year. Values above line indicate that survival increased in presence of crabs, values below the line indicate that crabs had negative impact.

Changes in predation by *Nucella lapillus* in the presence of crab predators

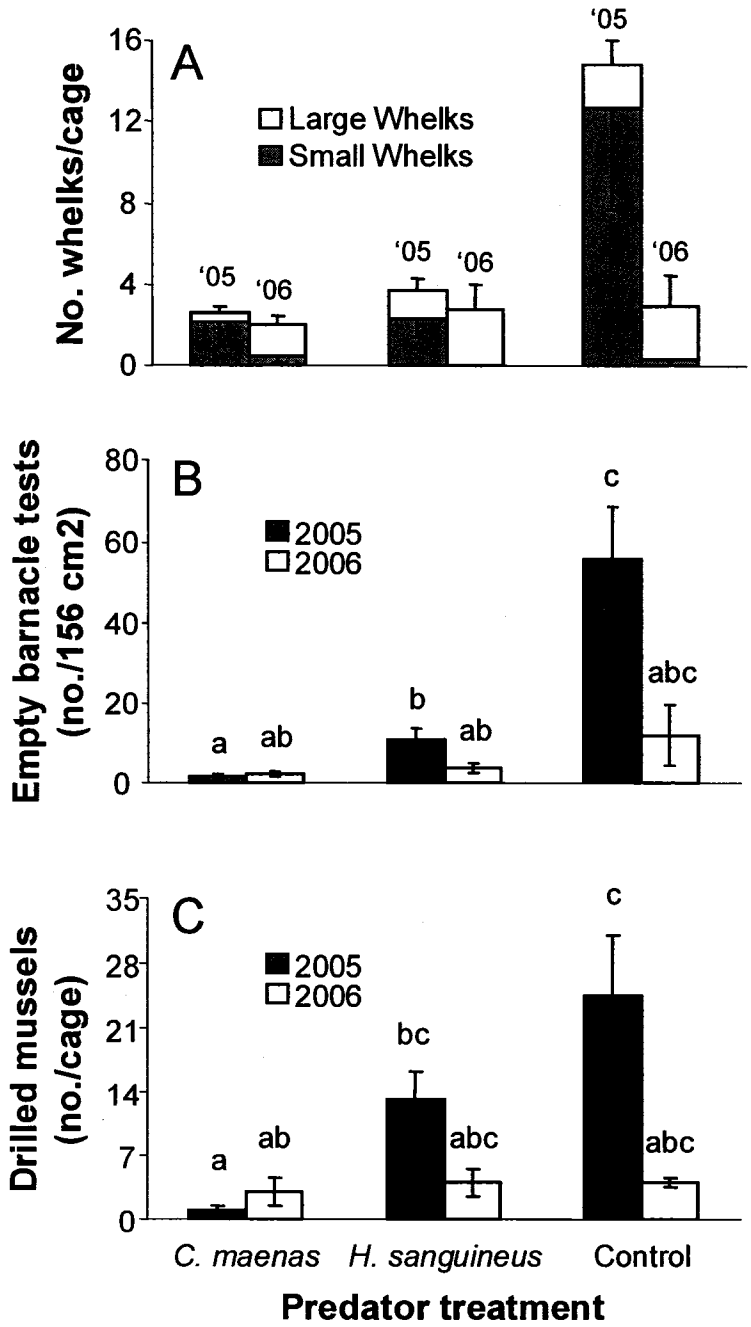

Figure 6.2 A) Final number of large and small *N. lapillus* in cages with 10 *C. maenas*, 10 *H. sanguineus*, or no crabs in both years. B) Final density of empty barnacle tests on rocks inside cages. C) Final number of mussel shells with drill holes. Bars are means ± SE (n=8 in 2005, n=4 in 2006 predator treatments, and n=3 in 2006 control treatment). Letters above bars give results of Tukey's tests.

Population level impacts of *C. maenas* and *H. sanguineus*

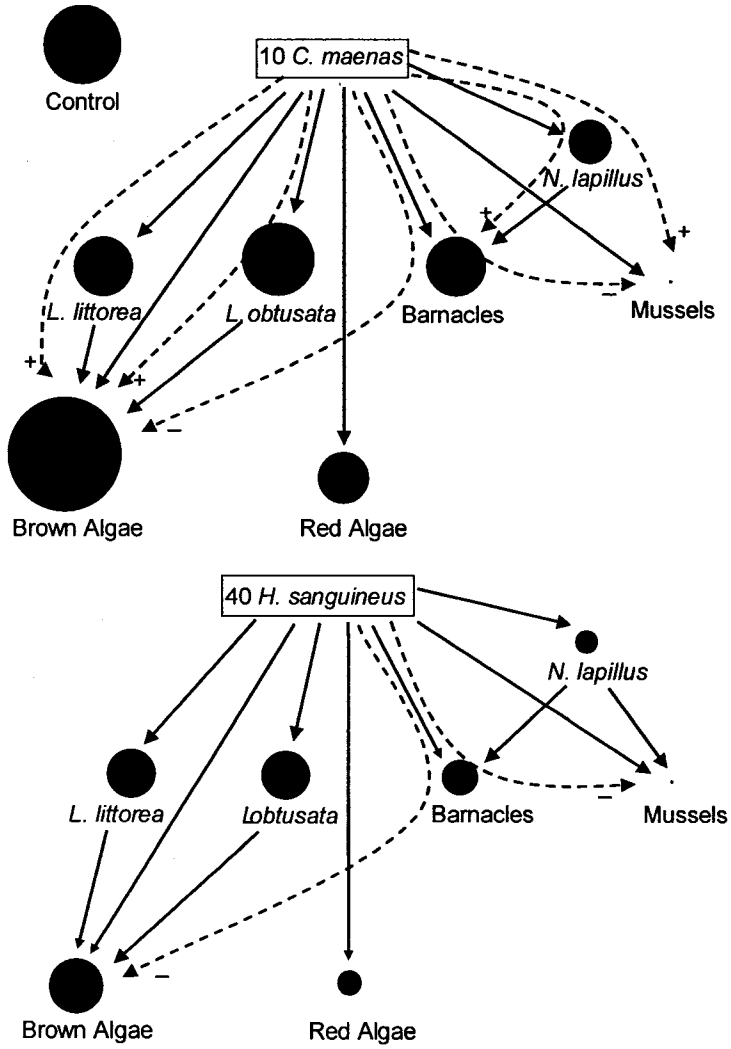

Figure 6.3 Relative effects of *C. maenas* and *H. sanguineus* as quantified in 2006 experiments when natural differences in population size are incorporated. Circle size gives survival relative to controls (incorporating both direct and indirect effects). While results are from the 10 *C. maenas* and 40 *H. sanguineus* treatments, cannibalism decreased geometric mean densities to 7.7 ± 0.3 *C. maenas* and 30 ± 1.9 *H. sanguineus*. Solid lines show direct trophic interactions (all have negative affects on prey). Dashed lines illustrate both density and trait mediated indirect effects. Arrows end at the species affected and show the sign of the interaction. The pathways of indirect interactions are demonstrated by the community member that the arrows pass through en route to the affected species. Positive indirect effects shown for *C. maenas* occurred more weakly with *H. sanguineus* as the top predator. However, the influences of these indirect effects are negligible compared to the large direct, negative trophic effects, and are thus not shown for simplicity.

CONCLUSIONS

Results of this study have provided important information on the invasion ecology of two conspicuous marine invaders, *C. maenas* and *H. sanguineus*. Results also contribute to our understanding of multiple predator effects and species redundancy.

Invasion Ecology of *C. maenas* and *H. sanguineus*

Previous studies have noted the displacement of *C. maenas* with the advancing invasion of *H. sanguineus* (Lohrer and Whitlatch 2002a, Kraemer et al. In Press). Despite claims that this replacement is not occurring within the central Gulf of Maine (Tyrrell et al. 2006), I found that the density of *H. sanguineus* is indeed increasing. Tyrrell (2006) reported a 10:1 ratio of *C. maenas*:*H. sanguineus* on New Hampshire's coast, and that eight years of sampling (dates unspecified) revealed no changes in the relative abundances of these species. However, while the densities of both species are highly variable across short distances (Fig 5.2), I found that overall the densities of the two species were approximately equal on the New Hampshire coast (Fig. 5.1). Further, I noted a general increase in *H. sanguineus* and a decrease in *C. maenas* (particularly juveniles) over the duration of my study at Odiorne Point, NH (2002-2006, Griffen, pers. obs.), one of the same sites used by Tyrrell (2006). Different findings of these two studies may have resulted from different sampling protocols or types of habitat examined. All sampling for my study was conducted in sites with extensive intertidal boulder fields which are highly preferred by *H. sanguineus*. While it is uncertain whether *H.*

sanguineus will replace *C. maenas* at this and other Gulf of Maine sites to the same extant that it has in Long Island Sound, patterns of species abundance reported here (Fig. 5.1) are reminiscent of southern sites and certainly imply that this species replacement is well under way.

Consumption of settling *C. maenas* megalopae by *H. sanguineus* is potentially responsible for this species replacement (Lohrer and Whitlatch 2002a). My study demonstrates additional mechanisms that may also be contributing to *C. maenas*' decline. *C. maenas* consumes fewer mussel prey when *H. sanguineus* is present (Fig. 3.1, 4.2, 5.4, 5.6), resulting in lower growth rates (Fig. 5.7). This may increase mortality by increasing the time necessary to achieve a size refuge from predation/cannibalism (deRivera et al. 2005), and could also potentially decrease population growth rates by increasing time to maturity, or by decreasing size at maturity (Twombly and Burns 1996). Further, although conspecific interference can greatly reduce mussel consumption by *C. maenas* (Smallegange et al. 2006, Griffen and Delaney, In Prep), gut contents of freely foraging crabs in the southern Gulf of Maine revealed *C. maenas* mussel consumption is reduced more by interactions with *H. sanguineus* than with conspecifics (Fig. 5.4). This is likely due to much higher densities of *H. sanguineus*, and thus more frequent interactions.

Populations of *C. maenas* in other regions are self regulating, with cannibalism increasing with population density (Moksnes 2004). It is possible that the *C. maenas* population on the North American east coast was also at a self-regulating "equilibrium" before the introduction of *H. sanguineus*, and that interactions with this new invader have tipped the scale through a combination of mechanisms (predation, exploitative competition, interference competition, etc.) to the detriment of *C. maenas*.

Finally, several studies have measured per capita consumption rates and impacts of small densities of adults of these two species in order to compare their community-wide impacts (Tyrrell and Harris 1999, Lohrer et al. 2000, Lohrer and Whitlatch 2002b, DeGraaf and Tyrrell 2004, Tyrrell et al. 2006). My studies demonstrate that population level effects of these two species on the invaded community depend on temporally variable prey abundance and on population densities of the two predators. Thus, comparisons of the impacts of the two species based on simplified experiments may not accurately represent impacts under more natural conditions. Further, differences in the degree of conspecific interference result in very large densities of *H. sanguineus* (Griffen and Delaney, In Prep) that are capable of very large negative impacts on prey communities (Fig. 6.3 and Lohrer and Whitlatch 2002b).

Multiple Predator Effects

My study demonstrated that documenting the presence or absence of multiple predator effects within a given system may not be sufficient, as these effects can vary across demographic groups (Fig. 1.1, habitat types (Fig. 2.3), prey densities (Fig. 3.2), and predator densities (Fig. 4.2). Further, the relative strength of these effects can be predicted under different conditions. However, given the number of conditions that could potentially exist with many sizes of individuals dispersed over heterogeneous landscapes, measuring differences in multiple predator effects under every conceivable situation is impractical. Thus, when a range of conditions exists (such as the range of *C. maenas* and *H. sanguineus* densities that also covary with prey density), using observational data may be more practical and may provide the necessary information to

understand interactions. As an example, gut contents of freely foraging crabs demonstrated that after prey density was accounted for, increasing the density of heterospecific predators had no impact on mussel consumption by *H. sanguineus*, but had a negative impact on mussel consumption by *C. maenas* (Fig. 5.4). This was true despite the use of a broad range of crab sizes and both sexes in the analysis.

When variable conditions are not a consideration (as may be the case in agroecosystems where habitat is relatively homogeneous and predators and prey have nonoverlapping generations), the experimental design proposed in Chapter 3, and used in Chapters 1, 3, and 4 that combines aspects of both the additive and substitutive experimental designs can provide more information than either the additive or substitutive design alone. The combined design not only indicates when multiple predator effects occur, but indicates their strength relative to nonindependent effects of multiple conspecific predators.

Species Redundancy

This study measured both the per capita redundancy of these species on amphipod prey (Ch. 1) and the population redundancy of these species on the entire prey community (Ch. 6). Results from Chapter 1 indicate that per capita redundancy differs with ontogeny and can depend largely on the intensity of interference interactions between individuals. Previous studies have also examined per capita impacts of these species, and have arrived at the opposite conclusions that *C. maenas* has stronger per capita impacts (Lohrer and Whitlatch 2002b), and that *H. sanguineus* has stronger per capita impacts (DeGraaf and Tyrrell 2004, Tyrrell et al. 2006). Results here indicate that

when population level impacts are examined (i.e., when natural population demographics of these crabs are examined) across the entire prey community and over long periods of time, individual differences in food preference and feeding rates are minimized and impacts of these species are very similar when they are at similar predator densities (Fig. 6.1). However, when the large differences in population densities that are naturally observed in many areas (Griffen and Delaney, In Prep) are considered, *H. sanguineus* has much larger impacts than *C. maenas*, and these differences are consistent across the entire prey community (Fig. 6.1).

Results here also indicate that species redundancy can vary temporally (and likely spatially as well) with changes in the prey community (comparison of Fig. 6.1 – comparison of 10 crabs of each species in 2005 and 2006). This is in contrast to a previous study in which two predatory salamanders had equivalent impacts on prey, regardless of initial prey densities (Morin 1995). Differences in results of the present study may be due to the presence of a third predatory species, the carnivorous whelk *N. lapillus*, and large indirect effects caused by changes in *N. lapillus* predation that differed between predator crab treatments, but were only present when barnacle and mussel prey were abundant (Fig. 6.4). In contrast, predatory effects in Morin's study were due solely to the two species of salamander being compared. Thus species that are redundant when comparing direct trophic effects may not be redundant when each elicits different behaviors, and therefore different indirect effects, in other community members.

In summary, the invasion of *H. sanguineus* may continue to have large impacts on the native prey community. These impacts may indeed be larger than those seen from *C. maenas*. However, differences in the effects of the two species are not solely a

consequence of differential per capita impacts. Rather, they result largely from 1) weaker conspecific interference for *H. sanguineus* than for *C. maenas* that allows *H. sanguineus* to achieve larger population sizes, 2) weaker influence of heterospecific interference for *H. sanguineus* than for *C. maenas* in areas where these species overlap and interact, and 3) weaker indirect effects elicited by *H. sanguineus* that dampen the impacts of other consumers (predatory and herbivorous snails) in areas where *C. maenas* is abundant.

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